

FISHERIES RESEARCH BOARD OF CANADA

Translation Series No. 717

Salmo salar Lin., its parasitic fauna and  
its nutrition in the sea and in fresh waters.

A parasitological-biological study

By Friedrich August Heitz

Original title: Salmo salar Lin., seine Parasitenfauna  
und seine Ernährung im Meer und im Süßwasser.  
Eine parasitologisch-biologische Studie.

Inaugural-Dissertation to attain a Doctor's Degree  
at the Philosophical Faculty of the University  
of Basle. Stuttgart. 139 pp. 1917.

Translated by Translation Bureau (MV)  
Foreign Languages Division  
Department of the Secretary of State of Canada

Fisheries Research Board of Canada  
Biological Station, St. Andrews, N. B.

1966

SALMO SALAR LIN.,  
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Submitted by  
Friedrich August HEITZ  
from Basle

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Stuttgart 1917  
E. Schweizerbart'sche Verlagsbuchhandlung  
Nägele & Dr. Sproesser

T o m y b e l o v e d p a r e n t s

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Natural Sciences of the Philosophical Faculty  
upon application by Professor Dr. Fr. ZSCHOKKE  
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Basle, January 26, 1916

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\* Translator's note: the figures in brackets refer to the pages in the original text

I. Introduction

(1)

1. Preface

On the basis of his intensive studies, Friedrich MIESCHER (66) makes the following statement:

"From the time it leaves the sea until it has spawned, the Rhine salmon does not eat, and usually not even afterwards."

Friedrich ZSCHOKKE (110, 111, 112, 114) tried to furnish parasitological proof for MIESCHER's statement by inferring from the qualitative and quantitative composition of the parasitic fauna of Salmo salar in various waters the nutritional habits of the fish in the sea and in the various rivers. He reached the following conclusion:

"Salmon does not take in any food in fresh waters, at least not while ascending and spawning."

Since the publication of these two reports, many more have been published by English, Scottish and Dutch researchers, in particular, which in part reject, in part agree with the above views formulated on the basis of accurate and thorough studies. Until today opinions differ on the feeding or fasting of salmon in fresh waters.

It appeared therefore desirable to continue ZSCHOKKE's studies on a large scale to achieve definite results. Another reason for this study was also the fact that the abundance of salmon in the Rhine is decreasing slowly on account of increasingly smaller spawning grounds. By dams of all sorts of factories, but particularly by the many power stations, the spawning grounds of the salmon which used to ascend the Aare, Reuß and Limmat Rivers as far as the Alps, have been restricted to the short distance between Augst and Basle in the Upper Rhine. 2

For this reason and the one mentioned previously I started studies on the salmon, and put myself a question which I tried to answer first for the Rhine salmon, and then also for salmon from other waters, namely the question:

Can inferences as to the nutritional habits of Salmo salar be drawn from the parasitic fauna of the Rhine salmon and from the parasitic faunas of salmon of other waters, and by comparing these faunas with each other?

Or, to express it in more general terms:

What is the significance of parasitological-faunistic findings for ~~nutrition~~ biological reflections? on nutrition? 5A

I started my studies at the end of the summer term of 1912.

The conditions prevailing here permitted my collecting sufficient fish material only during the autumn and winter months. Only a few intestines were examined during the spring and summer months, and those were mainly of non-Swiss salmon. A total of 200 salmon intestines was examined which were of the following origins:

From the Upper Rhine	128	) River area of the Rhine
From the Middle Rhine	8	
From the Lower Rhine (including the mouth of the Rhine)	17	170
From the Moselle River (Alzet)	17	
From the Weser River	21)	
From the Loire River	5	30
From Norway	4)	
	<hr/>	
	Total:	200

Professor Dr. Fr. ZSCHOKKE was good enough to put at my disposal the material collected by him, for statistical purposes, and I shall make use of it particularly in the chapters on the frequency, number and origin of the salmon parasites. Here I would also like to include the following material in order to give a complete review of all the parasites collected in Basle:

- 1889: 45 salmon fish from the Rhine
- 1891: 129 " " " " (including the 45 from 1889)
- 34 from the Baltic Sea

1896: 5 from the Middle and Upper Rhine

1896: 3 from the Dutch Rhine

7 10 from the North Sea

Total: 181 salmon fish

I have not included the 20 salmon specimens examined by HAUSMANN (35) in 1897 because his parasitological examination dealt only with trematodes.

If we add the salmon examined by ZSCHOKKE and by myself for parasites, we get a total of 381 salmon, 307 of which came from the Rhine and 74 of which originated from other waters, partly from rivers, partly from the sea.

The material to be examined - the fish intestines - were put at my disposal most willingly by fishmongers in Basle. Whenever possible, the intestine was cut off at the anus and pulled out with the head, together with all connected organs such as liver, spleen, agenital glands, etc. In this manner I at least obtained the complete intestines and presumably also the majority of parasites in the body cavity. It was of course impossible to ascertain what remained behind in the body cavity, but in my opinion it was not much. Most of the parasites were encapsulated in or on the various glands, on the intestine and between the pyloric appendages.

Now and then I obtained intestines also from inns.

Several times I took blood from a fresh catch of Rhine salmon on the spot to examine it for blood parasites, but the results of such tests were always negative.

I would like to take this opportunity to express my heartfelt gratitude to everyone who has assisted this study by his advice or cooperation. Above all I wish to thank my venerated teacher, Professor Dr. Fr. ZSCHOKKE, from the bottom of my heart for his unfailing devotion in supervising my work, encouraging and assisting me with valuable advice and permitting me to make full use at any time of his extensive collection of literature of parasites. Thanks to him I was able to use the facilities of the Zoological Station at any time, even during the war which caused considerable delay in my work, and also during the long vacations; I was thereby enabled to continue my work in spite of having to devote much time to my duties in the border control service 1914/15. I derived the greatest possible benefit from his extensive experiences in the field of parasitology, especially during our working together on the parasites of Salmonidae from Kamchatka.

I am greatly indebted to Dr. C. von JANICKI for his vivid interest in the progress of my studies and his <sup>ready</sup> advice and cooperation.

I would also like to thank the two fishmongers in Basle,

Mr. CHRISTEN and Mr. GLASER; especially Mr. Christen and his firm supplied me in the most generous way with an abundance of material for my studies and always tried to comply with all my requests.

2. The nutrition of Salmo salar at various developmental stages, in the sea and in fresh waters

In the following I would like to summarize our knowledge on the nutritional habits and food of the salmon at its various developmental stages and in its various habitats (sea and rivers). We will see that opinions still differ widely on all questions concerning the nutrition of Salmo salar.

(a) The young fish in fresh waters: Depending on the temperature of the water and on general climatic conditions, the young salmon hatch from the egg membrane after 45 - 148 days. They are born as tiny fish, with the vitelline sac still attached to them which is their first source of food. Their mobility increases 5 by the gradual resorption of the vitellus, until finally they are able to look for food themselves. They find the rich mud and soil fauna of a mountain stream ready for them to feed on. The bigger the fish becomes, the more insatiable is its appetite. It does not feed so much on the plancton which occurs only in scarce amounts in flowing water, but mainly on the living beings under stones and on plants. The following list will give an idea of the variety

of food of the young salmon:

According to HOEK (40, 41): Larvae of Chironomus, Baetis, Simulium, Perla, Hydropsyche, Cloe, Ephemera; diptera, insects; rarely Ancylus (house with snail); insect eggs. No plancton: neither Daphnia nor copepodes.

According to FRITSCH (24): Baetis, Hydropsyche, Cloe, Chironomus, Simulium, ants, Glossosoma, Potamanthus, Oligoplectrum, Perla, Sericostoma; Rhizotrogus (beetle). Rarely and in contrast to HOEK: Asellus aquaticus; Ancylus and spiders. Now and then also salmon eggs which the young fish rob <sup>from</sup> eggs laid by adult fish.

According to Mc.INTOSH (64): Beetles, flies, insect larvae and small crustaceans.

According to SELIGO (92): Midges and other insect larvae; also smaller species of crustaceans.

(b) Nutritional habits of the descending young salmon: After attaining a length of 11 - 21 cm, the young fish start migrating towards the sea, always taking in food on their way; this food, however, gradually changes in its composition. HOEK has shown that in streams and rivers they feed mainly on insects and insect larvae. The closer the fish get to the sea, however, the more they feed on plancton. In the mouth of the river the young salmon lives on the abundant fauna of brackish water. It feeds on crustaceans of all

kinds, above all on Gammarus locusta, Crangon vulgaris and the schizopod Mysis vulgaris.

(c) Nutritional habits of the salmon during his first

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stay in the sea: As soon as they reach the sea the young salmon disappear in the depths and can no longer be observed. Based on the scarce findings, we can only speculate on ~~its~~ <sup>their</sup> nutrition there. Various authors have tried to throw light on that part of the life cycle of salmon, with varying success. All researchers agree, however, that salmon, both European and American and Asiatic, are extremely voracious in the sea.

MURRAY (39) has tried to demonstrate where and when salmon feed in the sea. He suspected a certain connection between the <sup>two</sup> facts that when the catches of herring along the coast are poor, the number of salmon ascending the streams is also small, and he did find such a connection. On the border between shallow water and the actual deep sea, at a depth of 180 - 200 m, there lies a mud zone which is the habitat of vast numbers of molluscs and crustaceans. The main and inexhaustible "hunting grounds" lie north of Scotland as far as Norway. Tidal movements and storms which turn up the sea down to its very bottom, carry the inhabitants of that mud zone, particularly schizopods and copepods, to the higher layers of water where they fall prey to the hungry herring and young salmon.

According to MURRAY's (39) studies, that source of food seems to have failed to materialize, and both species of fish did not have enough food; they remained in the sea therefore to prolong the period of nutrition instead of appearing at the coasts.

(d) Nutritional habits of older salmon in the sea: Older and old salmon which have made many a journey up and down the streams, also live in those hunting-grounds which were described above. They attack above all smaller and weaker animals appearing there. Large numbers of herring, smelts, sticklebacks and garpikes fall prey to the voracious salmon.

We know the Baltic sea salmon to undertake frequently long journeys to find food. SELIGO (92) assumes even that they occasionally leave the basin of the Baltic Sea to look for suitable food in the North Sea. Large numbers of sprats, herring, Tobias fish, sticklebacks and also young codfish are found in their stomachs. 7

Incidentally, these feeding places are frequented also by the various enemies of the salmon, namely dolphins, sharks and also seals.

In general it can be said that the salmon in the sea usually stays in greater depths, i.e. colder water, not far from the coast, feeds voraciously there, grows rapidly in size and weight and thus

gathers strength, preparing for its first, or last, journey into fresh waters.

At present there are still doubts about the actual period during which Salmo salar feeds so voraciously without interruption. Presumably it does not go on its first journey upstream before the age of 3 or 4 years. Likewise, we do not possess any definite knowledge on the number of migrations within the life cycle of a salmon and in particular on the periods in the sea between the individual journeys through fresh waters. American opinion has it that salmon migrate every 2 years, according to Swedish reports, (LANDMARK 1892, [22]), every year. MIESCHER (66) reports differently on the Rhine salmon: according to him, the salmon lives through a maximum of 3 spawning seasons or migrations; in between the individual trips there may be intervals of 2 years for males, and 2-3 years for females. That researcher draws the following/<sup>general</sup> conclusion: " The migration habits seem to differ from river area to river area; they perhaps depend on the length of the way in the river and on the range of distribution in the sea."

(e) Nutritional habits of the salmon ascending the streams to spawn: As yet we know little on this part in the life cycle of the salmon. Generally speaking, we may say that during the spawning season the salmon, similar to all Salmonidae and many other migratory fish, goes entirely or almost entirely without food.

"The Rhine salmon performs the most amazing and thorough fasting test known to physiology(MIESCHER)". According to numerous studies, the salmon seems to fast for long periods.

Even before MIESCHER, several researchers had pointed out 8 that salmon fast in fresh waters. After MIESCHER the discussion on this question was continued. Below, I have summarized observations and views of other authors and myself which might help to solve this problem.

I would like to start with some reports of earlier date:

RONDELET (1507-1566): Salmon become fat in the rivers.

WILLOUGHBY (1635-1676): The returning salmon are thin.

KNOX (44): Salmon do not take any food in the rivers after they have been to the sea.

OWEN(81): Freshwater salmon feed voraciously, but have the habit of vomiting all the food when caught.

v.SIEBOLD (93): "I cannot but mention here that until now examinations and descriptions of the digestive tract of salmon fish have completely disregarded the fact that these fish go without food for weeks before and after their spawning season, and that their stomach contracts very much."

Mc.INTOSH (64): Tay salmon does not fast completely, but takes in food occasionally, although at greater intervals and not

voraciously, as is proved by the stomach contents. The latter consists only of the well-known tough mucus. Ten times parts of the skeletons of fish, small pieces of crustaceans and insects were found. More than 100 salmon were examined.

BARFURTH (4): 20 Rhine salmon were examined. Esophagus and stomach contained only white, tough mucus. Nothing was found in any part of the digestive tract which indicated the intake of food (spawning salmon). The same results from September to December. Only now and then wood particles or plant fibres. In 3 winter salmon from the Lower Rhine remains of food (parts of insects, insect larvae, cycloid scales) were found. According to private communications of fishermen, (Clupea harengus) parts of fish/were found occasionally in salmon from the mouth of the Rhine, but not <sup>from</sup> farther upstream. BARFURTH also quotes the following on this question: BERTRAM (1865) - examined 9 hundred of fish and found traces of food only rarely. BUCKLAND: Examined large number of salmon, always found intestines empty of food, frequently with intestinal worms attached.

Let us now quote more recent results:

MIESCHER (66): The Rhine salmon does not take in food from the time it ascends from the sea until it has spawned, and usually not even afterwards. Marine salmon (North and Baltic Seas) feed voraciously. Esophagus and stomach contracted already in salmon from

the mouth of the river. Remains of food rare. Occasionally small stones, grass stalks, plant stems in esophagus or stomach; they were swallowed with the river water. Once in the small intestine a fairly large insect larva, but completely undigested and intact. Only tough mucus in esophagus and stomach, also in the intestine. Never any traces of digestion. Gall bladder always empty.

Takes in food very rarely when returning to the sea after spawning. Only once remains of two fish (presumably Leuciscus) were found in the stomach. Stomach slightly distended, with some thin secretion with acid reaction. After spawning salmon revert to the type of marine salmon in spite of extreme emaciation. Degenerative phenomena disappear.

ZSCHOKKE (112): In esophagus, stomach and intestine only mucus. Among 129 salmon, plant fibres and a slightly digested Gammarus pulex were found in the small intestine one time each. Remains of a sand eel found once in the stomach of a Dutch salmon.

FRITSCH (24): Ascending Elbe salmon always with empty stomach; only yellow tough mucus. Reported to snap for insects in resting places (as a pastime). After spawning, as "Tuloc" (= vagabond), taking in food now and then - various insects and insect larvae. Once an old salmon was imprisoned together with 2 young salmon; it ate two of them.

HOEK (38): With few exceptions (7 of approximately 200),

all salmon caught in Holland have an empty stomach. Lumina close together in stomach which has folded walls; intestinal epithelium 10 destroyed, even in winter salmon. Regression of digestive tract starting already in the sea. Fish after spawning have completely empty stomach. Only once a Gammarus pulex was found; presumably it had entered the gullet with respiratory water and was swallowed. No remains of food in intestine, only sticky mucus. No adipose cover on pyloric appendages. No longer any parasites.

PATON and ARCHER (83): Scottish and English salmon do not take any food in fresh water. Degeneration of gastric and intestinal mucous membranes. Decomposition bacteria in the intestine of ascending salmon, particularly in the upper course of the river, numerous because destroying acids lacking. Fat disappears. Before the fish reach the sea again, they are completely restored to their previous condition.

GULLAND (31): Examined 118 salmon (Scotland) from sea, river mouth, river (ascending or descending). In fresh water, stomach and intestine pathologically degenerated so that intake of food is impossible. Gastric mucous membrane degenerated. Inflammation spreading more the farther the fish migrate. Gall bladder empty; it starts filling slowly only when the fish are descending, a sign that the liver also starts functioning again. Stay in fresh water is not responsible for these conditions as they start already in

almost  
the sea and because/all organs have been regenerated before the descending salmon reach the sea, at least the stomach. Spawning process is the determining factor.

BROWN (14): In the sea: clear fluid in stomach with acid reaction. Food. No yellow mucus. In fresh water: intestine filled more or less with yellow mucus. Inflammation of mucous membranes. Adsorption of fat. No food. Results: in fresh water salmon are not in a position to be as voracious as in the sea, but they may feed occasionally, depending on the climate, location, temperature and amount of water.

BARTON (5): Inflammation of epithelium in intestine and stomach due to post-mortal effect. In healthy fish intestinal epithelium completely intact. No pathological phenomena in fish from 11 the upper course of the river, either. His views are opposed to those maintained by GULLAND.

GULLAND (32): Reply to BARTON. Insists on his findings which were also made before the death of the fish.

BARTON (6): After spawning the salmon can again take in food; they do it, too, although in small quantities. Adipose globules in the intestine prove it. They feed on infusoria and other lower animals.

TOSH (99): In a river as short as the Tweed, salmon do not feed at all, except under unusual circumstances which force them to stay in fresh waters for a prolonged period.

McMURRICH: Fish of the genus Oncorhynchus in North America and Alaska never take food in rivers. Intestine contracted, stomach hardly discernible.

SCHMIDT:(116): The species of Oncorhynchus do not feed at all in the Asiatic rivers (Amur, etc.). Intestine and stomach contracted, mucous membranes degenerated.

By way of conclusion, I would like to add to these different observations and results my own experiences made with salmon from various rivers.

Norway salmon:(4 specimens) from the sea: 3 of them contained many remains of food, partly digested fish, scales, otoliths in intestine and stomach. Only very little mucus. No food remains in the fourth specimen; ovaria<sup>es</sup> were already fairly big.

Weser salmon (21 specimens): all of them ascending or spawning - never food remains in stomach or intestine. In esophagus and stomach, slightly watery mucus, in pyloric part of intestine and small intestine, frequently granular, tough mucus.

Loire salmon (5 specimens, 4 of them ready to spawn, from the upper course, and one of them with little developed ovaries from the lower course): no traces of food. Only tough, yellow-white to orange-yellow mucus.

Rhine salmon (including Moselle): Of the 170 salmon examined,

only 12 had plant particles in esophagus or stomach, included in mucus: wood fibres, grass stalks, wood particles (one half of a 12 pencil), husks of grain. There were also occasionally small stones, pieces of coal, soil, etc. Animal parts were found only in 3 salmon: in an Upper Rhine salmon, cocoons of Phryganeidae (Micrasema minimum); in one Middle Rhine salmon, remains of mites; in a salmon from the Upper Rhine which had spawned, a small trout, slightly affected by digestion, in esophagus and stomach.

All the other 156 salmon did not show any traces of food in their digestive tract. It should be stressed that in agreement with HOEK's findings, none of the 17 salmon from the mouth of the Rhine contained remains of marine food in the intestine.

Doubtlessly all the plant particles entered the gullet with respiratory water and accidentally passed into the esophagus. Such objects are swallowed and remain stored, completely covered by mucus, mostly in the esophagus, more seldom in the stomach. Frequently the mucus in the esophagus and stomach was watery and almost transparent, which is due to the entering of water.

Even the animal bodies might have passed into the stomach accidentally, for in addition to plant particles, also animals, floating soil species such as Phryganeidae larvae and mites, might get into the respiratory water of a fish and thus be swallowed by

it. The intestine with the small trout came from a large spawner of the Upper Rhine after spawning; it had been caught at the end of December 1912 near Augst above Basle. I had the opportunity to examine the genital organs of that salmon. Its ovaries were already more compact (immediately after spawning they are loose and greatly elongated). Here and there a few eggs were left in the ovaries.

Apart from these few foreign bodies mentioned above, esophagus, stomach and intestine contained, as already stated, the well-known mucus the appearance of which has already been described by McINTOSH, MIESCHER, FRITSCH, HOEK and many other salmon researchers. My attention was attracted by the intestinal mucous 13 membrane, particularly that of the small intestine, which very frequently looked burned.

I would like to mention one circumstance which has been used as proof for both the fasting and the feeding of salmon in fresh water and has led to the opinion that salmon feed in certain rivers, but fast in others. This circumstance is catching salmon with a fishing rod which has become a real sport in Scotland.

North Sea:

NORDQUIST (according to ZSCHOKKE, 112): In Finland the behaviour of the fish differs from river to river; in some they feed, in others they do not, which manifests itself in fishing.

LÖNNBERG (58): Baltic Sea salmon which ascend the Swedish streams cannot be caught by fishing rod. He doubts whether the fish caught in Norway and Scotland by fishing rod are mature; he thinks they are sterile forms.

NORDQUIST (75): Salmon are caught by fishing rod also on the coasts of the Baltic Sea; they tear themselves away and keep the hook in their gullet.

Scotland:

1901: It is reported from Scotland that fishing of salmon by rod is flourishing (22).

1902: Reference is made to the Norwegian rivers which allegedly are better suitable in their lower course for salmon fishing, more than the Scottish rivers where hardly any salmon is caught any more (22).

Canada:

1900: The salmon rivers of Labrador were widely advertised, promising the fishing enthusiasts an abundance of salmon (22).

McMURRICH (65): The Oncorhynchus species of North America cannot be caught by fishing rod.

Rhine area:

1875: An Englishman caught a large salmon on his fishing

rod near Schaffhausen (22).

1897: A salmon (?) was caught with a fishing rod in the Neckar (22).

1897: A large salmon was caught with a fishing rod in the basin of the Rhine Falls (Schaffhausen), but it was able to tear itself away again (22).

1899: A salmon was caught in the Nahe (tributary of the Rhine) with a fishing rod by means of a small fish.(22).

1899: Similar catch as above near Murg (Upper Rhine) (22)

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1910: Salmon very numerous in the Wiese (tributary of the Rhine below Basle). An angler caught 3 specimens with a fishing rod within one hour (23).

Let us finally see how MIESCHER (66) thinks about this question.

"I have repeatedly heard it said that during the spawning months, salmon are occasionally caught with a fishing rod in the small streams near Basle (e.g. in the Wiese river), which usually is not possible here. Although I have not been able to obtain any definitely proved information to that effect, I dare not, in view of my experiences, to deny such a possibility completely - but only for the time after spawning."

applicable  
I cannot draw any generally conclusion from these findings

so briefly outlined here. It only seems to me that fishing for salmon will be always successful where they can still migrate into small streams, gathering in comparatively large numbers in low-level waters. If they are barred from such small streams, they have to spawn in main streams where they naturally distribute more; this very reason already seems to make fishing more difficult.

Let us summarize in a few sentences the information collected on the nutritional habits of the salmon in the sea and on its journey upstream:

(1) Young salmon in fresh waters first feed on the contents of their vitelline sac, then on the insect larvae living on the bottom of the river or stream, and finally on plancton.

(2) The young salmon migrating to the sea gets accustomed to brackish food in the mouth of the rivers and gradually also to marine food.

(3) In the sea the salmon usually do not travel much. They stay at their hunting grounds which, if possible, are close <sup>to</sup> their native river. The only exception is perhaps the Baltic Sea salmon. Marine food consists mainly of small fish.

(4) When the salmon ascend from the sea, they presumably stop taking food altogether. This is closely linked with the <sup>initial</sup> ~~starting~~ development of their genital organs and therefore may start already in the sea.

(5) The following observations speak in favour of the view 15 that the ascending spawners or milters do not take any food:

(a) The digestive tract was always found to be empty, without any remains of food. If such remains are found occasionally, they are not digested at all or only incompletely.

(b) The observations by MIESCHER on the morphological and physiological changes in the intestine, the liver, spleen and gall bladder of the ascending Rhine salmon.

(6) In the descending salmon, the digestive tract slowly regenerates (according to MIESCHER, 66, PATON and ARCHER, 83). Above all the stomach resumes its normal function, also the liver, which is indicated by the fact that the gall bladder starts refilling slowly (GULLAND, 31).

(7) Descending salmon can take in food, but do so only <sup>after</sup> ~~at~~ long intervals, without choosing and presumably completely inactively.

The above reflections and observations on the nutritional habits of salmon in fresh waters show that the problem has not been finally solved. This paper will try and help reaching a solution by parasitological means. In this capacity it is a continuation and extension of the studies by McINTOSH (64), ZSCHOKKE (112), FRITSCH (24) and TOSH (99).

With the help of comparative faunistic studies of the parasitic fauna of salmon from various seas and river systems, I would like to draw conclusions on the nutritional habits of the fish in its various habitats.

3. Chronological review of authors who have examined Salmo Salar for parasites or have at least mentioned and described parasites from salmon<sup>1</sup>

1602	ALDROVANDUS, U.	} Hirudines (81) pisces maiores, et praesertim Salmones mirabiliter inficientes.	
1610	GESNERUS, C.		
1686	WILLOUGHBY.		Les sangsues (81) incommodent beaucoup les saumons.
1741 oder 1756 1746	GEOFFROY, M. SPÖRING, D.	Taenia spec. (18) ( <sup>see</sup> siehe: de Bomare Val. 1780). Taenia continua-plana fulcis longitudinalibus (17).	France Frankreich. Sweden Schweden.
<sup>2)</sup> 1751	GISLER (GISOLAR).	Kiefenwurm des Lachses (Lernaea) (75).	Sweden Schweden.
1756	GEOFFROY, M.	des sangsues (81), qui incommodent beaucoup les saumons.	
1775	MÜLLER, L.	Lernaea salmonea L.in. (75).	Taxonomy Systematik.
1776	MÜLLER, F.	75. Bothriocephalus solidus (24).	"
1777	MÜLLER, F.	75 (nach GISOLAR 1751). Echinorhynchen (70).	"

<sup>1</sup> The figures correspond to those in the subsequent list of parasites. The first occurrence of a parasite is indicated by its full name and by the figure given to it in the above-mentioned list.

<sup>2</sup> Papers which mention salmon parasites, but which were not available to me in their original version.

1779	BLOCH, F.	Taenia crassa (1).	Rhein.	Rhine
1780	DE BOMARE, VAL.	18 (dans les entrailles des vers plats). 81.	Frankreich ?	France ?
1780	MÜLLER, F.	1. Fasciola varica (33). Fasciola salmonis (34)? Echinorhynchus salmonis MÜLL. (64).	Ostsee.	Baltic Sea
1781	PALLAS, S.	1.	Rheinu. Elbe	Rhine and Elbe
1782	HERMANN, J.	Echinorhynchus salvelini (63).	Rhein.	Rhine
1782	GOEZE, E.	1. Cucullanus (46). Echinorhynchus quadrirostris GZ. (27).	Quedlinbg.	
1786	BATSCH, G.	1. Taenia nodosa BATSCH (32).	Systematik.	Taxonomy
1787	GOEZE, E.	1. 27. 46.	"	"
1787	MÜLLER, F.	Taenia, Echinorhynchus, Cucullanus, Fasciola.	"	"
1788-1806	MÜLLER, F.	33. 64.	"	"
1788	V. SCHRANK, P.	1. 27. 63.	"	"
[1788	GMELIN, ED.	1. 24. 27. 33. 46. 63. 64. 75.	"	"
1801	RUDOLPHI, A.	46.	"	"
1802	RUDOLPHI, A.	1. 24. 33.	"	"
1802	BOSC, G.	1. 27. 33. 46. 63. 64.	"	"
1803	ZEDER, H.	1. 27. 33. 46. 63. 64.	"	"
1809/10	RUDOLPHI, A.	1. 24. 27. 33. 46. 63. 64. Distomum crenatum? (45). ? nodulosus (63?). Cucullanus? (59).	"	"
1815	OKEN, L.	1. 27. 33. 46. 64. 75.	Naturgesch.	Natural history
1816	DE LAMARK, M.	1. 33. 75.	Naturgesch.	"
1819	RUDOLPHI, A.	1. 24. 27. 33. 46. Distomum appendiculatum Rud. (35). Echinorhynchus fusiformis Rud. (62).	Systematik.	Taxonomy
1819	LEUCKART, S.	1. 27.	"	"
1821	WESTRUMB, L.	62. 63.	"	"
1828	DE BLAINVILLE M.	1. 27.	"	"
1836	SCHINZ, R.	75. Kratzer, Band-, Kappen- und Plattwürmer.	Naturgesch.	Natural history

Acantocephala, tapeworms, flatworms and \*

1838	DRUMMOND, L.	Tetrarhynchus grossus RUD. (= solidus DRUM.) (30).	Irland	Ireland
1839	CREPLIN, H.	Cucullanus elegans (58).	? Ostsee.	? Baltic Sea
1844	BELLINGHAM, O.	1. 23. 32. Ascaris clavata RUD. (47)	Irland.	Ireland
1845	DUJARDIN, F.	1. 27. 33. 35. 46. 47. 58. 62. 63. 64.	Systematik.	Taxonomy
1845	GURLT, H.	1. 24. 27. 33. 35. 46. 62. 63. 64.	"	"
1847	CREPLIN, H.	30.	? Ostsee.	? Baltic Sea
1849	CREPLIN, H.	30. Bothriocephalus imperfectus cysticus (3).	Systematik.	Taxonomy
1851	DIESING, M.	1. 24. 27. 33. 46. 47. 58. 63. 64.	Systematik.	"
1853	BAIRD, W.	1. 30. Tetrarhynchus rugosus BAIRD (26).	England.	England
1854	DIESING, M.	1. 30.	Systematik.	Taxonomy

\* Translator's note: No German definition of the term "Kappenwürmer" could be found, also no English translation. Consultation with various scientists was equally unsuccessful. Literally, it means "hooded worms".

1858	NEUMANN R.	63.	Ostpreußen.	East Prussia
1863	DIESING, M.	1. 30.	Systematik.	Taxonomy
1863	Mc. INTOSH, C.	1. 27. 33. 46. 63. 64. Gregariniform animal (10). Tetrarhynchus spec. (28). Distomum tereticolle RUD. (36). Distomum spec. (54). Ascaris spec. (57). Lepeophtheirus Strömii BAIRD (76).	Tay.	
1866	GIEBEL, C.	1. 24. 33. 46. Cysticercus spec. GIEBEL (21).	Systematik.	"
1866	OLSSON, P.	1.	Ostsee.	Baltic Sea
1867/68	OLSSON, P.	33. 35. Distomum ocreatum RUD. (34).	Ostsee.	"
1868	KESSLER, K.	1. 64.	Onegasee.	Lake Onega
1871	V. BENEDEK, J.	1. 33. 34. Distomum reflexum CREPL. (38).	Nordsee.	North Sea
1872	V. HERING, ED.	1. 33. 46. 62. Echinorhynchus Anthuris Duj. (65).	Württemberg.	Württemberg
1876	OLSSON, P.	35.	Ostsee.	Baltic Sea
1878	V. LINSTOW, O.	46.	Hameln-Weser.	
1878	V. LINSTOW, O.	1. 24. 27. 30. 33. 34. 35. 38. 46. 47. 58. 63. 64. Bothriocephalus cordiceps (LEIDY) (4).	Systematik.	Taxonomy
1879	MONIEZ, R.	Leuckartia nov. gen. MONIEZ (= Abothrium crassum) (1)?	Lille.	
1881	MONIEZ R.	1?	Lille.	
1884	V. LINSTOW, O.	46.	Hameln-(Weser).	
1885	PRENANT, A.	46. as intermediate host of	Mosel.	
1886	KÜCHENMEISTER, F.	Salmo salar als Zwischenwirt von Bothriocephalus latus BREMS ??		
1888	V. LINSTOW, O.	Tetrabothrium minimum nov. spec. (larva) v. LINST. (22).	Göttingen.	
1889	KERBERT, C.	Findet d. Larven v. Bothriocephalus latus BREMS trotz Fütterungsversuchen nicht in Salmo salar	Niederlande.	Netherlands, does not find larvae of Bothriocephalus latus Brems in Salmo salar in spite of feeding tests 18

1889	ZSCHOKKE, FR.	1. 30. 33. 38. 46. 47. Bothriocephalus spec. ZSCHOKKE (5, 6, 7, 8). Rhynchobothrium paleareum (RUD.) (25). Distomum Miescheri ZSCHOKKE (39). Echinorhynchus spec. ZSCHOKKE (71).	Rhein Rhine
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<sup>2</sup> see footnote on page 26

1889	V. LINSTOW, O.	1. 5. 6. 7. 8. 33. 39. 46.	Systematik.	Taxonomy
1889	LÖNNBERG, E.	1.	Schweden.	Sweden
1890	ZSCHOKKE, FR.	Bothriocephalus osmeri v. LINST. (5). 6. 7. 8.	Rhein.	Rhine
1890	FATIO, V.	Zitiert die Funde von FR. ZSCHOKKE (siehe 1889).	Naturgesch.	Natural history, quotes findings by...
1891	ZSCHOKKE, FR.	1. 4. 5. 6. 7. 8. 22. 24. 25. 27. 28. 30. 32. 33. 34. 35. 36. 38. 39. 44. 46. 47. 58. 63. 64. Ascaris adunca RUD. (48). Ascaris communis DIES (49). Ascaris aculeati v. LINST. (50). Ascaris angulata RUD. (51). Echinor- hynchus agilis RUD. (66). Echinorhynchus gadi O. F. MÜLL. (67).	Rhein, Nord- und Ostsee.	Rhine, North and Baltic Seas
1892	MATZ, FR.	1. 5. (nach ZSCHOKKE).	Systematik.	Taxonomy
1894	FRITSCH, A.	1. 27. 30? 33. 46. 47. 64. 75. Scolex pleuronectis O. F. MÜLLER (31). 34. Argulus coregoni THON. (77) Piscicola geometra LYN. (79). 38.	Elbe.	
1894	STILES u. HASSALL.	1 (aus Berlin). Bothriocephalus spec. (9) (aus England).	amerik. Sammlung.	American collection
1896	ZSCHOKKE, FR.	1. 5. 6. 7. 8. 25. 27. 30. 31. 33. 34. 38. 46. 47. 48. 49. 63. 66? 79. Bothriocephaluslarven (11). Te- trarhynchus spec. ZSCHOKKE (29). Neorhynchus rutili (MÜLL.) (61). Echinorhynchus spec. ZSCHOKKE (72). Ascaris spec. I. II. ZSCHOKKE (55. 56).	Rhein und Nordsee.	Rhine and North Sea
1897	HAUSMANN, L.	33. 34. 35. 38.	Rhein.	Rhine
1898	MÜHLING P.	1. 34. 62. 63. 64. 67.	Ostpreußen.	East Prussia
1899	HOEK, C.	47. 63? Cystobranchnus respirans TROSCII (80).	Holland.	
1901	LINTON, E.	Ascaris spec. (larva) LINT. (54).	Amerika.	White Sea
1901	V. LINSTOW, O.	63.	Weißes Meer.	
1902	ZSCHOKKE, FR.	Abothrium rugosum (BATSCH) (2).		Baltic Sea
1902	SCHNEIDER, G.	1. Echinorhynchus spec. (larva) SCHNEID. (73).	Ostsee.	
1903	SCHNEIDER, G.	1.		
1904	STAFFORD, J.	33. 35. Sinistrophorus simplex (RUD.) (40). Lecithaster ho- lthyrophorus (OLSS.) (11).	Canada.	
1904	HOFER, BR.	1. 4. 22. 24. 27. 30. 33. 34. 35. 38. 39. 46. 47. 58. 63. 64. 76. Ler- naeopoda carpionis KROBY. (78) Fischegel (81). fish leech	Systematik.	Taxonomy

1905	TOSH, J.	1. 22. 27. 30. 33. 34. 39. 46. 63. 67. Taenia spec. (larva) TOSH (19). Tetrabothrium spec. (larva) TOSH (23). Ascaris acuta RUD. (52). Ascaris obtusicaudata ZED. (53). Echinorhynchus angustatus RUD. (58).	Tweed.
1907	WARD, B.	from aus <i>Oncorhynchus nerka</i> : 1.	Alaska.
1908	WARD, B.	from aus <i>Salmo salar-sebago</i> : 1. Proteo- cephalus pusillus WARD (15). Proteocephalus (larva) WARD (16). Bothriocephalus larven (12). Cestodenlarve (20). Azygia sebago WARD (37). Nematodes A. B. (60).	Nordamer. North America
1908	PFEILER, W.	62. 64.	Systematik. Taxonomy
1910	WEGENER, G.	75.	"
1911	LÜHE, M.	1. 5. 6. 7. 8. 24. 25. 27. 30. 33. 34. 38. 39. 63. 64. Lecithaster gib- bosus (RUD.) (42). Hemiurus Lühei ODHNER (43).	Systematik.
1913	BIELER, W.	64.	
1914	LA RUE, G.	15.	
1914	ZSCHOKKE, FR. und HEITZ, A.	from aus <i>Oncorhynchus nerka</i> : 46. 67. Bothriocephalenlarven (13). Pelichnibotrium caudatum ZSCHOKKE (14). Echinorhynchus caenotomis HEITZ (69). from aus <i>Oncorhynchus keta</i> : 1. 14. 46. 67. Henneguya Zschokkei GURL. (74). from aus <i>Oncorhynchus tshawytscha</i> : 14. 27. 30. 46. from aus <i>Oncorhynchus kisutsch</i> : 74.	Ost-Kam- tschatka. East Kamtchatka

Table I.

List of salmon parasites mentioned in the chronological review

1. Endoparasites:	
a) Cestodes:	
1. <i>Albothrium crassum</i> (Bloch) (= <i>Taenia crassa</i> Bloch 1779 = <i>Leuckartia</i> Mon. 1879?).	23. <i>Tetrabothrium</i> spec. Tosn. 1905.
2. <i>Albothrium rugosum</i> (Bartsch) 1902.	24. <i>Schistocephalus gasterostei</i> (Fabr.) 1776.
3. <i>Bothriocephalus imperfectus</i> cysti- cus CREPL. 1849.	25. <i>Tetrahynchus palcaceus</i> Rud. 1889.
4. <i>Bothriocephalus cordiceps</i> LEIDY 1878.	26. <i>Tetrahynchus rugosus</i> BAIRD. 1853.
5. <i>Bothriocephalus osmeri</i> v. LINST 1891.	27. <i>Tetrahynchus quadrirostris</i> (GZE.). 1782.
6. <i>Bothriocephalus</i> spec. I. ZSCHOKKE. 1890. 1891.	28. <i>Tetrahynchus</i> spec. Mc. INT. 1863.
7. <i>Bothriocephalus</i> spec. II. ZSCHOKKE. 1890. 1891.	29. <i>Tetrahynchus</i> spec. ZSCHOKKE. 1896.
8. <i>Bothriocephalus</i> spec. III. ZSCHOKKE. 1890. 1891.	30. <i>Coenomorphus grossus</i> LÜHE. 1838.
9. <i>Bothriocephalus</i> spec. STILES- HASSALL. 1894.	31. <i>Scolex pleuronectis</i> MÜLL. 1893.
10. Gregariniform anim. Mc. INT. 1863.	32. <i>Triacnophorus nodulosus</i> (PALL.). 1786.
11. <i>Bothriocephalus</i> larven ZSCHOKKE. 1896.	b) Trematodes:
12. <i>Bothriocephalus</i> larven WARD 1908.	33. <i>Derogenes varicus</i> (MÜLL.). 1780.
13. <i>Bothriocephalus</i> larven ZSCHOKKE- HERRZ. 1914.	34. <i>Brachyphallus crenatus</i> (RUD.). 1780? 1867.
14. <i>Pelichniobothrium caudatum</i> ZSCHOKKE. 1914.	35. <i>Hemiusurus appendiculatus</i> (RUD.). 1819? 1904.
15. <i>Proteocephalus pusillus</i> WARD. 1908.	36. <i>Azygia tereticollis</i> (RUD.). 1863.
16. <i>Proteocephalus</i> larva WARD. 1908.	37. <i>Azygia sebago</i> WARD. 1908.
17. <i>Taenia continua plana</i> fulcis longi- tudinalibus SPÖRING. 1746.	38. <i>Distomum reflexum</i> CREPL. 1871.
18. <i>Taenia</i> spec. DE BOMARE. 1741 u. 1756. 1780.	39. <i>Distomum Miescheri</i> ZSCHOKKE. 1889.
19. <i>Taenia</i> spec. Tosn. 1905.	40. <i>Sinistrophorus simplex</i> (RUD.). 1904.
20. Cestodenlarven WARD. 1908.	41. <i>Lecithaster bothryophorus</i> (OLSS.). 1904.
21. <i>Cysticercus</i> spec. GENEL. 1868.	42. <i>Lecithaster gibbosus</i> (RUD.). 1911.
22. <i>Tetrabothrium minimum</i> v. LINST. 1888.	43. <i>Hemiusurus Lühej</i> ODN. 1914.
	44. <i>Distomum</i> spec. Mc. INT. 1863.
	45. <i>Distomum crenatum</i> Rud.? 1809 u. 1810.
	c) Nematodes:
	46. <i>Ascaris capsularia</i> Rud. (= <i>Cu- cullanus</i> GZE). 1782.
	47. <i>Ascaris clavata</i> Rud. 1844.

1 The figures in front of the names correspond to those in the chronological review. The years mentioned are those in which the parasite was found in salmon for the first time.

- |  |   |
|--|---|
| 48. <i>Ascaris adunca</i> RUD. 1891.             | 69. <i>Echinorhynchus caeniformis</i> HERTZ. 1914.  |
| 49. <i>Ascaris communis</i> DIES. 1891.          | 70. <i>Echinorhynchen</i> MÜLLER. 1777.   |
| 50. <i>Ascaris aculeati</i> v. LINN. 1891.       | 71. <i>Echinorhynchus</i> spec. ZSCHOKKE. 1889.   |
| 51. [ <i>Ascaris angulata</i> RUD. 1891.         | 72. <i>Echinorhynchus</i> spec. ZSCHOKKE. 1896.   |
| 52. <i>Ascaris acuta</i> RUD. 1905.              | 73. <i>Echinorhynchus</i> spec.? SCHNEID. 1902.   |
| 53. <i>Ascaris obtusocaudata</i> ZED. 1905.      | e) <i>Myxosporidia</i> :  |
| 54. <i>Ascaris</i> spec. LINT. 1901.             | 74. <i>Henneguya Zschokkei</i> GÜLL. aus <i>Oncorh. kisutsch</i> und <i>Onc. keta</i> . 1914. |
| 55. <i>Ascaris</i> spec. I. ZSCHOKKE. 1896.      | 2. Ectoparasiten.   |
| 56. <i>Ascaris</i> spec. II. ZSCHOKKE. 1896.     | i) Copepoda:  |
| 57. <i>Ascaris</i> spec. Mc. INTOSH. 1863.       | 75. <i>Lernaeopoda salmonea</i> LIN. 1751. 1775.  |
| 58. <i>Cucullanus elegans</i> ZED. 1839.         | 76. <i>Lepeophtheirus Strömii</i> BAIRD. 1853.  |
| 59. <i>Cucullanus?</i> RUD. 1809/1810.           | 77. <i>Argulus Coregoni</i> THOR. 1893.   |
| 60. <i>Nematodes</i> A. B. WARD. 1908.           | 78. <i>Lernaeopoda carpiois</i> KROEY. 1904.  |
| d) <i>Acanthocephala</i> :                       | g) <i>Hirudinea</i> :   |
| 61. <i>Neorhynchus rutili</i> (MÜLL.). 1896.     | 79. <i>Piscicola geometra</i> LIN. 1894.  |
| 62. <i>Echinorhynchus truttae</i> SCHRANK. 1819. | 80. <i>Cystobranchus respirans</i> THOSCH. 1899.  |
| 63. <i>Pomphorhynchus laevis</i> (ZOEGER). 1782. | 81. <i>Hirudines-1602</i> (= <i>sangsues</i> 1686 = <i>Fischegel</i> 1904).                   |
| 64. <i>Echinorhynchus salmonis</i> MÜLL. 1780.   |   |
| 65. <i>Echinorhynchus Anthuris?</i> DUJ. 1872.   |   |
| 66. <i>Neorhynchus agilis</i> (RUD.). 1891.      |   |
| 67. <i>Echinorhynchus gadi</i> O. F. MÜLL. 1891. |   |
| 68. <i>Acanthocephalus lucii</i> (MÜLL.). 1905.  |   |

fish leech

#### 4. History of the research into the parasitic fauna of salmon

##### (a) Endoparasites:

During the first decades of the 18th century, a period when numerous scientists examined the various animal classes for parasites and parasitology became a systematic, organized branch of science on the basis of purposeful studies, the first salmon parasites were found. Salmo salar, an excellent food fish and a migratory fish travelling regularly through the various media, fresh water and salt water, (almost) challenged studies and attracted the attention of scientists at an early stage. In the course of almost 170 years, up to the present day, this giant among the freshwater fish became the subject of numerous studies in biology, anatomy, histology and parasitology. Jp. 22

The first parasite was found in 1746, the year when H.D. SPÖRING (94) mentioned, when finding a tapeworm in a woman, that there are worms "that live in fish"; among the infected species listed by him was also salmon. The description given by that scientist of Taenia continua plana fulcis longitudinalibus - as he called the parasite - allows no definite interpretation and comparison with any of the salmon parasites known today. BRAUN (12) interprets Taenia as Ligula larva, an interpretation which is hardly the true one because since then Ligula has never been found in salmon. I am rather

inclined to believe - and the description and particularly the drawing by SPÖRING of the parasite found in salmon which differs from those by the same scientist on the same Plate of the worms from Abramis, Leuciscus, Gobio etc. seem to confirm this - that the Swedish scientist was dealing with the common tapeworm of salmon, Abothrium crassum. There is a simple explanation for the fact that the parasite was found in the body cavity. It happens not infrequently, and I myself observed the same phenomenon occasionally, that in dead salmon the intestine is severely inflamed, inflated, and the intestinal wall therefore tears very easily. Often such an intestine was torn and the intestinal parasites lay in the body cavity which might of course give the impression as if the worms had always lived there.

So much on the first parasitic find in Salmo salar. It also disproves the statement by WARD (103) that in 1726 FRISCH had found a parasite in a stickleback which later was found also in Salmo salar. In that case the parasite was really a Ligula, but in my opinion it is not identical with the one encountered later by SPÖRING. Therefore SPÖRING's find must be regarded as the first in Salmo salar and as the first in general of an endoparasite which parasitizes also salmon.

The next chronological report of a salmon parasite cannot be pinpointed as to the year. A French dictionary published by

VAL. DE BOMARE (11) in 1780 contains the following passage:

"Ils ont (les saumons) dans ses entrailles de vers plats. Les continuateurs de la 'Matiere médicale de Mr. GEOFFROY' 23 trouverent, il y a quelques années, dans le ventre d'un saumons un taenia d'une longueur extrême et d'une grande blancheur, lequel était encore plein de vie quatre jours apres la mort."

The French doctor and natural scientist Et.M. GEOFFROY referred to in the above passage published his main work "Tractatus de materia medica" in 1741. His successors, various French scientists, published another edition of his work in 1756-1757, presumably with additions and improvements. Unfortunately, I could not find the passage quoted by BOMARE in that second edition.

A short paper on fish parasites by a man from Strasbourg, however, has greater significance for our purposes than those questionable French communications. Professor J. HERMANN (37), most likely a medical man, conducted studies in natural science in addition to his profession. When examining various Rhine fish, he also found parasites which he drew for his own entertainment; he added his comments to those drawings. His attention having been drawn to the papers by PALLAS and MÜLLER published just then, he used his notes for a short report which he published in 1782. His findings must date back to much earlier years because he mentions the work "Elenchus Zoophytorum" by P. S. PALLAS, published in 1766, as

already known, the "Prodromus Zoologica Danica" by Fr. MÜLLER (1776), on the other hand, as not yet published. His studies must therefore have been conducted between 1766 and 1776. We shall not be far wrong if we assume that he made his findings in 1770.

That year is of such special importance to us because it is the first time we hear about a parasite from Rhine salmon. I am quoting the relevant passage from HERMANN's paper:

"I found some of these worms (Echinorhynchus salvelini SCHRANK = Pomphorhynchus laevis [ZOEGER]) in the stomach of salmon. According to the usual habit of this genus of worms, they were firmly attached in the inner mucous membrane."

The next findings of Rhine salmon parasites are those by BLOCH (10) in 1779 and by PALLAS (82) in 1781. Both scientists found the common tapeworm of salmon, Abothrium crassum, and published it under the name Taenia tetragonoceph or Taenia crassa. 24

In the years 1776-1800 O. F. MÜLLER (73,74), GOEZE (29), PALLAS (82), etc. published their works which laid the foundations for helminthology. There, we find most of the salmon parasites known today as the most common ones, although often badly described and depicted. RUDOLPHI's (87,88) publications (in 1809, 1810 and 1819) summarized all discoveries of parasites from Salmo salar up to that time.

parasitological

In 1838, while conducting studies on fish from Ireland and the Irish coast, DRUMMOND (19) described two parasites from Salmo salar: Tetrarhynchus grossus RUD. from the body cavity, and a new species, also from the body cavity, which he called Tetrarhynchus solidus. (According to more recent findings, they are identical; see "Systematic Part" under Coenomorphus grossus).

In 1863, McINTOSH (64) examined salmon migrating to the Scottish river Tay for spawning (for parasites). He found 11 species of endoparasites in more than 100 salmon. A large number of those parasites were potamophilous which induced the scientist to believe that salmon take in some food in fresh waters.

In 1879 and 1881, MONIEZ (69,70) published observations on a salmon cestode which he introduced/as the type specimen/of a new genus, Leuckartia nov.gen. on account of various anatomical characteristics. LÜHE (59) abolished this parasitic species because he considered it synonymous with Abothrium crassum (BLOCH) (see "Systematic Part").

In 1886 and the following years, scientists started disputing about the life cycle of Bothriocephalus latus BREMS in which Salmo salar played a questionable part of intermediate host infecting man. KÜCHENMEISTER (46) maintained that man could infect himself/by eating raw or half-cooked fish, and made salmon, eels, pikes and other food fish responsible for that circumstance without, however,

substantiating his statements by any tests or findings. His opponents, in particular BRAUN (13), GRASSI and FERRARA (30), held the view that it was above all the pike which acted as intermediate host, but under no circumstances Salmo salar. ZSCHOKKE (111) also dealt with 25 this question and studied various Bothriocephalus larvae which he found in Salmo salar; but none of the larvae showed any relation to Bothriocephalus latus.

In 1889, 1890 and 1891, ZSCHOKKE published the results (110, 111, 112) of his examinations of salmon from the Rhine and the Baltic Sea for parasites. As I shall refer repeatedly to those publications in the course of my paper, I need not discuss them in detail here.

In 1894, FRITSCH (24) published his anatomical-biological study on the Elbe salmon. At the end, that report lists several species of parasites found occasionally in the Elbe salmon.

In 1896, ZSCHOKKE (114), on the occasion of a parasitological examination of the Rhine fish species, again reported on several new parasites he had found in salmon from the Rhine and the North Sea.

In 1897, HAUSMANN (35) described several trematodes from the species of Rhine fish examined in 1896 (see above), and also mentioned the flatworms found in salmon.

In 1905, TOSH (99) reported on the parasitic fauna which he

had encountered in his studies of the salmon from the Scottish river Tweed. He found 15 species of parasites, most of them of marine origin.

Parasitological data on American salmon species are very scarce. In 1907, WARD (102) reported that he had found Abothrium crassum in the Alaska salmon, Oncorhynchus nerka.

The same author published a parasitological paper in 1908 on Salmo salar sebago, a North American salmon species which has adapted itself completely to life in fresh water and never gets into contact with the sea. Its parasitic fauna is only of potamophilous origin (7 species).

The above paper also mentions several finds made by BEAN in Oncorhynchus nerka and by RUTTER in Oncorhynchus tshawytscha; cestodes, trematodes (?) and parasitic copepods were found (see Systematic Part).

In 1914, an extensive study was published by ZSCHOKKE and HEITZ (116) on the parasitic fauna of various salmon species (Oncorhynchus nerka, O.keta, O.tshawytscha and O.kisutsch) from the east of Kamtchatka. The examination of this abundant parasitic material (6 species of cestodes, 4 of nematodes, and 2 of acanthocephalals as well as one of myxosporidia) yielded the interesting result that the parasitic fauna, that is to say its composition and

nature, of the salmon species in Eastern Asia is similar to that of European salmon.

Apart from the publications mentioned above, dealing mainly or entirely with the parasitic fauna of salmon, there is a large number of scientific papers which, in addition to many other species of parasites, hosts and intermediate hosts, also discuss Salmo salar and its parasites more or less. The authors of such papers and the species of salmon parasites they have either described or found for the first time and described, are listed in the chronological review; it suffices therefore to merely enumerate their names here: 1866-1867, OLSSON (78); 1872, HERING (36); 1876, OLSSON (79); 1868, KESSLER (43); 1893, OLSSON (79); 1898, MÜHLING (72); 1900, HOEK (38); 1902 and 1903, SCHNEIDER (90,91).

(b) Ectoparasites:

It remains to refer briefly to the ectoparasites of salmon of which only a few are known. Data on such findings are much older than those on endoparasites, which seems to be due to the ease with which this type of parasites can be noticed. Frequently, the mass occurrence of these bloodsuckers caused severe damage among the populations of food fish; fishermen felt these repercussions and they therefore tried to combat them with all possible means. Even spiritual help was accepted, as appears from the following passage taken from

the great work by U. ALDROVANDI (1) (1522-1600) and is rendered here in a free, abridged translation as follows:

"Leeches often attack the salmon in winter by attaching themselves to their mouths or their tails and even cause them to jump with pain. The salmon try to detach their enemies, but they usually hardly save their lives, frequently dying from the inflicted injuries. The saintly bishop of Lausanne<sup>1</sup> caused incantations to 27 be collected from Holy Scriptures and publicly proclaimed on certain days against the leeches which torture the salmon and inflict deadly injuries on them."

In the end, ALDROVANDUS tells us from where he got his information:

"FELIX MALLEOLUS inquit, qui vixit circa annum Domine 1554 (should read 1454)"<sup>2</sup>.

This reference to the early knowledge of ectoparasites will suffice for our purposes. The literature of the 17th century mentions

<sup>1</sup> Presumably Guilielmus d'ECUBLENS who was bishop in Lausanne from 1221-1229. He is the author of the above-mentioned exorcisms against "all poisoned worms and snakes" which he commanded "never to crawl, nest and live again in them (rivers and lakes)".

<sup>2</sup> Felix MALLEOLUS is the famous Felix HÄMMERLIN from Zurich, doctor of Canonical Law, canon of Zurich and Zofingen. He lived from 1389-1464. He died in the prison of Lucerne where he wrote the "Tractatus de Exorcismis" shortly before his death. It says in that treatise: "Previously and now the bishops of Lausanne cursed the leeches which killed the salmon".

such parasites at several other occasions, but it seems that one scientist had copied the story by MALLEOLUS from another, only with his own respective remarks. "Les sangsues incommodent beaucoup les saumons" writes the Englishman WILLOUGHBY (107) in 1686; the same sentence we find in V. de BOMARE's (11) dictionary.

None of the other reports on ectoparasites date back so far. Most of these parasites were not discovered before the 19th century. Only Lernaeopoda salmonea LIN. seems to have been known since 1800. At least O.F. MÜLLER (73) in 1776 and the 12th edition of LINNE's (49) "Systema naturae" in 1775 mention the Swede GISLER or GISOLAR as the man who reported on "a Lernaea of the salmon" in 1751.

II. Systematic Part

1. Preliminary remarks

In order to simplify the systematic part as much as possible and at the same time follow a certain classification, I have used several abbreviations which should be explained right in the beginning to facilitate orientation. This classification and these abbreviations will be used throughout all the other chapters, too.

The parasites have been classified into the following groups depending on origin and main range of distribution:



In order to avoid enumerating all hosts for each parasite, 29 and yet to keep the list clearly arranged, I listed only the names of those hosts which the parasite concerned infests only in exceptional cases , e.g. Derogenes varicus parasitizes numerous marine fish, some migratory fish and 3 freshwater fish; the exceptions, in this case the freshwater fish, are listed by name.

Migratory fish are always listed by name. Short lists of hosts are always given complete.

In cases where a large number of marine or potamophilous hosts would have to be listed, only the individual orders of fish are mentioned to which the hosts belong. The figure behind the order <sup>or suborder</sup> refers to the number of species parasitized by the parasite.

Derogenes varicus, e.g. parasitizes 51 marine fish which all belong to the order of the Teleostei; among the hosts are 22 of the suborder Acanthopterygii, 1 of the suborder Pharyngognathi, 23 of the suborder Anacanthini, and 5 of the suborder Physostomi.

The list of hosts also gives the organs infested by the respective parasite, and in outline the geographical localities of the hosts. Both organs and localities are described in greater detail for migratory fish and in exceptional cases.

2. Endoparasites

Plathyhelminthes:

(a) Trematodes: Five <sup>types ?</sup> species of trematodes are found in Salmo salar which are of the following origin:

- α. Marine forms: 8 (4 of which parasitize the Rhine salmon)
- β. Marine-potamophilous forms: 1 (1 of which parasitizes the Rhine salmon)
- γ. Potamophilous forms: 2 (2 of which parasitize the Rhine salmon).

(α) Marine forms:

Distomum Miescheri ZSCHOKKE (Table 1, Fig.1). This parasite, discovered by ZSCHOKKE (110) in 1889 and infesting only 30 Salmo salar, shall be the first of the purely marine trematodes to be discussed. The range of this worm is extremely limited: the North Sea and the rivers <sup>flowing</sup> falling into it which the salmon frequent. The number of hosts is even smaller - only Salmo salar. ZSCHOKKE found this trematode in a few specimens of Rhine salmon, TOSH (99) in a similar number in salmon from the River Tweed in 1905, and FRITSCH (24) in the Elbe salmon.

In my extensive parasitic material I encountered Distomum Miescheri only three times, namely one time each in an Upper Rhine, Middle Rhine and Lower Rhine salmon. They always lived in the stomach

which was richly folded.

The parasite is immediately recognizable on account of its typical shape, already emphasized by ZSCHOKKE as characteristic feature, and it can thus be easily distinguished from the other salmon trematodes. The entire body is shaped like a written Latin E. It can therefore be easily divided into an anterior end of the body reaching from the oral sucker to closely behind the ventral sucker, and a posterior end of the body (caudal part according to ZSCHOKKE). The body of my largest specimen is 12 mm long.

Since ZSCHOKKE's description of this parasite contains all essential facts on shape, dimensions of body and of suckers, I need not go into detail here.

On its inner structure, however, I would like to add a few remarks and corrections.

Even ZSCHOKKE ~~himself~~ corrected himself with regard to the development of the intestine in his second publication on salmon parasites (112). The spherical, very muscular pharynx is followed by a sac-like extended esophagus. The intestine forks out into two parts approximately in the first third of the distance between oral and ventral sucker. The two parts themselves extend to the posterior end of the body in slight spirals. At approximately the middle of their entire length, caeca start protruding which rearward become

bigger and then smaller again towards the end of the two parts. ZSCHOKKE reports dorsal and ventral sacs. In my opinion this is not the case. In one of my specimens the intestine is completely filled with a brown-black mass - visible even to the naked eye - so that 31 it can be seen clearly that the two parts of the intestine have only dorsal ramifications.

The excretory pore lies at the end of the posterior end of the body. ZSCHOKKE has interpreted and described the course of the excretory vessels correctly.

ZSCHOKKE writes that the male and female genital passages end at a larger or smaller distance from each other, which LÜHE (61) considers very questionable. To clear these doubts, I examined 2 preparations left of ZSCHOKKE's material and my material carefully and reached the following conclusions:

Distomum Miescheri has only one genital pore which is located ventrally approximately on the level of the posterior oral sucker. The pore is surrounded by swollen margins. The entrance is followed by a bottle-shaped distension, the genital atrium, at the base of which lies the actual, joint orifice of the two combined genital passages. This strange arrangement may easily give the impression that there are two openings, for the pore is sometimes far away from the end of the Ductus hermaphroditus. It may be shifted

forward as far as beyond the middle of the oral sucker.

In all specimens the entire genital organs were still little developed, and what was already developed was almost always hidden by the two parts of the intestine coloured black by their contents.

There is nothing essentially new about the male organs. The oval testicles lie slightly before the beginning of the intestinal caeca. I cannot make any statements on the Vasa deferentia on account of the reason mentioned in the preceding paragraph. The seminal vesicle is an elongated sac which is approximately 0.540 mm long; it lies dorsally in front of the ventral sucker. The prostata part surrounded by prostata cells lies in front of the Ductus hermaphroditus into which the male and the female genital passages open. The excretory duct for male and female genital products, the Ductus hermaphroditus, is enclosed by the short, muscular cirrus pouch which, when relaxed, protrudes very slightly into the genital atrium.

The following can be said about the female genital organs. Behind the testicles lies the spherical ovary with a diameter of 1.705 mm. Adjoining it is the sausage-shaped Receptaculum seminis which is somewhat smaller than the ovary. It was impossible to ascertain whether a Laurer canal existed or not. On account of the two parts of the intestine, the vitellaria are hardly visible, but they lie behind the testicles and the ovary. Likewise, the course of

the uterus is invisible until a short distance before the ventral sucker, but it seems to extend rearward in transverse loops and then forward straight.

Nothing remains to be said about the ecology of this parasite as ZSCHOKKE (112) has already discussed this question. I fully agree with his view that Distomum Miescheri is a purely marine form.

Distomum reflexum ZSCHOK.nec.CREPL. Found only a few times and in small numbers in Rhine salmon by ZSCHOKKE (112) and HAUSMANN (35).

Sotfärtha only known hosts are Cyclopterus tumpus and Salmo salar. Development unknown. Geographical distribution limited to North and Baltic Seas.

Lecithaster gibbosus (RUD.). This is a purely marine parasite. I found it several times in Rhine salmon and in 2 specimens of Norwegian salmon, partly in the stomach, partly in the intestine, the usual habitat of this parasite in other hosts.

I have nothing to add to the detailed descriptions by LEVINSEN (48), ODHNER (77) and other authors. The following hosts are known for this parasite:

Marine fish:

<u>Teleostei:</u>	<u>Acanthopterygii:</u>	8	intestine)	Atlantic Ocean,
	<u>Pharyngognathi:</u>	2	"	(European and
	<u>Anacanthini:</u>	5	"	American coasts),
	<u>Physostomi:</u>	4	"	North and Baltic Seas

## Migratory fish:

<u>Salmo salar</u>	Stomach and intestine	Rhine; Norway
<u>Salmo trutta</u>	Intestine	Scandinavia
<u>Anguilla vulgaris</u>	"	"

Lecithaster bothryophorus (Olss.) which was found by STAFFORD (95) as a parasite of Salmo salar at the Canadian coast, 33 is presumably synonymous with Lecithaster gibbosus. Unfortunately STAFFORD did not make any detailed statements on shape and size of his parasite.

It is interesting to note that STILES and HASSALL (97) name Colymbus cristatus as another host. The marine trematode may have entered the bird intestine with food, with a migratory fish presumably playing the role of intermediate host.

Sinistrophorus simplex (RUD.). According to reports by STAFFORD (95), this parasite has been found in Canadian marine fish, among which Salmo salar is mentioned as the only migratory fish. It cannot be decided whether this species is synonymous with Distomum simplex RUD. because morphological details are lacking.

In any case, this parasite is a northern form of marine character. STAFFORD lists the following hosts: Acanthocottus scorpius, Gasterosteus aculeatus, Hemitripterus americanus, Phycis cuss, Scomber scombrus, Sebastes marinus and Salmo salar.

Hemiurus Lühei ODHNER. According to LÜHE (61), this parasite was found once in Leipzig in a salmon of unknown origin. From the list of hosts its marine character becomes obvious.

Marine fish:

<u>Acanthopterygii:</u>	4	Esophagus & stomach	)	North Sea. At-
<u>Anacanthini:</u>	2	" "	)	lantic Ocean
<u>Physostomi:</u>	3	" "	)	(European and American coasts)

Migratory fish:

<u>Salmo salar:</u>	Esophagus	Fish market in Leipzig?
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Brachyphallus crenatus (RUD.). Until recently, no other trematode group was as confused as that of the Hemiuridae (= Apoblema Duj.e.p.) because "various authors used different names for the same species or listed different species under one and the same name" (LÜHE,60).

RUDOLPHI (87), OLSSON (78,79), and MÜHLING (72) report on trematodes with anal appendages which they found in salmon and called Distomum appendiculatum. All details given by these authors on classification, locality and host have to be accepted with great caution. ODHNER (77) has proved that most of those finds (OLSSON) are not Distomum appendiculatum, but Brachyphallus crenatus. LÜHE (60) also stated that MÜHLING's finds, which he classified as Distomum, did not belong to that species, but to Brachyphallus. He also proved

RUDOLPHI's (87) report to be incorrect.

The same will apply to those reports by ZSCHOKKE (112), FRITSCH (24) and HAUSMANN (35) which classified all trematodes with anal appendages found in Salmo salar as Distomum appendiculatum.

According to LÜHE (60), Brachyphallus crenatus very often parasitizes the Baltic Sea salmon (Königsberg). ZSCHOKKE (112) also found his trematodes in salmon from the Baltic Sea. HAUSMANN (35) found trematodes in Rhine salmon which he classified as Distomum appendiculatum and Distomum ocreatum (no author mentioned; presumably Dist.ocreatum OLSS.nec.RUD.), but both species are synonymous with Brachyphallus crenatus. Most likely his finds will also belong to the latter species.

The same may apply to Dist.appendiculatum found by FRITSCH (24) in Elbe salmon, but it is not certain because we have neither picture nor description.

Occasionally I found a trematode species in Rhine salmon the structure, shape and size of which agree<sup>s</sup> in all details with the characteristics described for Brachyphallus crenatus by ODHNER and LÜHE.

As the synonymy is so complicated and information on localities so uncertain, it is very difficult to make definite statements on geographical distribution and hosts. However, we can

obtain a fairly clear picture from the facts we are certain of.

This parasite has approximately the following hosts:

Marine fish:

<u>Acanthopterygii</u> :	3	Esophagus & stomach)	Atlantic Ocean.
<u>Anacanthini</u> :	9	" "	) North and Baltic
<u>Physostomi</u> :	3	" "	) Seas. Mediterranean (rare)

Migratory fish:

<u>Salmo salar</u> :		Esophagus and stomach	North and Baltic Seas, Rhine, Elbe, &c.
<u>Osmerus eperlanus</u>	"	" "	Elbe, ? &c.
<u>Salmo trutta</u>	"	" "	?
<u>Acipenser sturio</u>	"	" "	Scandinavia

35

This shows that Brachyphallus crenatus parasitizes exclusively marine hosts and belongs to the northern fauna.

Distomum appendiculatum EUD. STAFFORD (95) found this parasite in a Canadian salmon, but does not describe it in detail. We can therefore not say whether he classified it correctly and Salmo salar is a host of Distomum appendiculatum, after all, or whether his find was also a Brachyphallus crenatus. WARD (103) has grave doubts about the correctness of the classification. Until other findings confirm or disprove it, however, we have to be satisfied with STAFFORD's identification.

I will not discuss the geographical distribution and the hosts of this parasite in any detail; it may suffice to say that Distomum appendiculatum is a marine form.

Distomum spec. McINTOSH 1863. McINTOSH (64) found a trematode in Salmo salar from the River Tay, but he did not identify or describe it. The parasite lived in the esophagus.

β. Marine-potamophilous forms:

Derogenes varicus (MÜLL.) Although this species of trematodes is predominantly marine, it occasionally infests also potamophilous hosts. This agrees with the fact that the most common parasites with the widest ranges of distribution are seldom forms of one or the other element. I would like to call to mind only Scolex pleuronectis and Ascaris capsularia. The hosts of this parasite are the following:

Marine fish:

<u>Acanthopterygii:</u>	22	Esophagus & stomach)	North & Baltic
<u>Pharyngognathi:</u>	1	" "	Seas, Atlantic
<u>Anacanthini:</u>	23	" "	Ocean (Europ. &
<u>Physostomi:</u>	5	" "	Amer. coasts),
			) Greenland

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Migratory fish:

<u>Salmo salar</u>		Esophagus & stomach	Rhine, North and Baltic Seas, Atlantic Ocean
<u>Salmo trutta</u>		" "	North Sea
<u>Osmerus mordax?</u>		" "	American coast
<u>Coregonus oxyrhynchus</u>		" "	?
<u>Anguilla vulgaris</u>		" "	?
<u>Acipenser sturio</u>		" "	Germany

Freshwater fish:

<u>Thymallus vulgaris</u>		" "	?
<u>Lota vulgaris</u>		" "	Scandinavia
<u>Coregonus Wartmanni</u>		" ?	"

by LEVINSEN (48)

The larval form of Derogenes varicus has been suspected/to

live in Harmothoe imbricata Lin. STAFFORD (95) mentions marine copepods (Acartia) as intermediate hosts.

I found Derogenes varicus fairly often in esophagus and stomach, but very rarely in the intestine. This trematode has more specimens in one salmon than any other salmon parasite. Frequently only a few specimens were found, but at other times more than 100. The worms always had a yellowish colour, which is caused by the eggs with which they are completely filled.

Derogenes varicus is known from numerous descriptions and drawings so that I need not discuss it any further.

γ. Potamophilous forms:

Crepidostomum farionis (MÜLL). As a northern parasite of purely potamophilous distribution, it is a rare guest of various fish of the family Salmonidae, as becomes clear from the following list of hosts:

Migratory fish:

<u>Salmo salar</u> :	Intestine	Rhine
<u>Salmo trutta</u>	"	Europe
<u>Coregonus oxyrhynchus</u>	"	Sweden

Freshwater fish:

<u>Salmo fario</u>	Intestine	Sweden
<u>Salmo salvelinus</u>	"	Germany
<u>Salmo fontinalis</u>	"	Canada
<u>Coregonus lavaretus</u>	"	Sweden
<u>Thymallus vulgaris</u>	"	"

STAFFORD (95) reports the strange fact that this parasite parasitizes an amphibian, Necturus (Menobranchus) maculatus (RAF.). The aquatic mode of life and nutrition of that animal may have caused it to become infected with the parasite. I shall not go into details on the varieties of Crepidostomum farionis on which STAFFORD reports.

Salmo salar is a new host of Crepidostomum farionis. I found this rare parasite once in the terminal intestine of a Rhine salmon. I have only little to add to the descriptions by RUDOLPHI (87) and in particular by OLSSON (77). The parasite is 2.484 mm long and has a maximum width of 1.080 mm. I am in a position to confirm the view ODHNER (77) had expressed on the number of papillae on the oral sucker. The specimen I found has 6 distinct tuberosities which originate frontally and laterally on the margin of the oral sucker.

We can only speculate on how Salmo salar acquired this purely potamophilous parasite. Perhaps with the respiratory water, perhaps through an intermediate host (if Crepidostomum farionis has one among the freshwater animals).

The geographical distribution of the parasite can be seen from the above list.

Azygia tereticollis (RUD.). In 1911, ODHNER (76) separated the trematode species known as Azygia tereticollis (RUD.)

into 2 species on the basis of the different sizes of the suckers and mainly on the basis of the different sizes and shapes of the pharynx, namely into Azygia tereticollis (RUD.) and Azygia robusta nov.spec. ODDH. The first species parasitizes predominantly Esox lucius, the second one lives in the intestine of various Salmonidae.

In 1863, McINTOSH (64) found a specimen of a Distomum species in a salmon from the River Tay; he identified it as Azygia tereticollis. Of course we can no longer say which of the two species he really found because we have no details. 38

In the stomach of a ~~xxxxxx~~ Rhine salmon I found an immature trematode which I identified as belonging to the genus Azygia on account of its size and shape and the development of its inner organs. The parasite is 12 mm long. The oral sucker has a diameter of 0.936 mm, the ventral sucker of 0.736 mm. The pharynx is 0.378 mm wide and 0.576 long, therefore it is almost twice as long as it is wide - a characteristic of the Azygia species from Esox lucius. We are thus dealing with Azygia tereticollis (RUD.) s.str. from Salmo salar.

This disagrees with ODHNER's (76) statements on the relationship between hosts and form of parasite. We, however, infer from this very interesting case that freshwater parasites are very rare and accidental guests in salmon, since Salmo salar has the Azygia species foreign to the Salmonidae, instead of the species Azygia robusta usually a parasite of Salmonidae.

We know as little about the mode of infection as in the case of Crepidostomum farionis. We can only repeat the same speculations.

With regard to the distribution of Azygia tereticollis, it is difficult to define it after ODHNER separated the species into two <sup>groups</sup> parts. If we eliminate localities where Azygia - presumably Azygia robusta - were found in Salmonidae (Salmo hucho in Wurttemberg, S. fario in Wurttemberg and in the Lake of Geneva, S. trutta in Sweden, S. lacustris in the Lago di Garda and S. salvelinus in Sweden), we still have sufficient clues to be able to say that Azygia tereticollis (RUD.) occurs almost all over Europe. This becomes obvious from the following list of hosts and localities:

Migratory fish:

<u>Salmo salar</u>	Stomach	Tay?, Rhine
<u>Anguilla vulgaris</u>	Branchial cavity	Swedish lakes

Freshwater fish:

<u>Acanthopterygii:</u>	2	Stomach	) Europe, Canada?
<u>Anacanthini:</u>	2	"	
<u>Physostomi:</u>	6	"	

(b) Cestodes: The order Cestoda accounts for the majority of the salmon parasites, with regard to both species and numbers. There is almost no Rhine salmon which, when opened, does not have a cestode of some form or species, either as larva or as mature worm. It is, however, strange that Salmo salar is not parasitized

by any other <sup>strobilar form</sup> form of Strobila but Abothrium crassum. The reason for this shall be only briefly referred to here, but discussed in detail in the biological-faunistic part; it is connected with the peculiar mode of life of Salmo salar, its life in the sea and in fresh waters.

A classification of the cestode parasites on the basis of their origin meets with various difficulties because mode of life, hosts and intermediate hosts are known of only a few species. The number of species parasitizing the salmon as larvae, on the other hand, is large, and their origin is difficult to ascertain. In order to follow a certain system in this part, just the same, I have included these larval forms and the species reported by various authors and considered as highly questionable forms in the group of marine parasites. It will become clear from the faunistic-biological part that I have not made any great mistake in doing so.

#### α, Marine forms:

Taenia spec. VAL. DE BOMARE (11). 1741, 1756, 1780.

I already discussed this species in the historical part. It is possible that it was a specimen of Abothrium crassum, a view further corroborated by the description of this worm, as no other cestode species is known from Salmo salar which has the same characteristics and lives in the intestine.

Taenia continua plana SPÖRING (94). 1746. This parasitic species has also been discussed in detail in the historical part. I would only like to repeat very briefly that, contrary to the view held by BRAUN (12), I do not consider this form as a larva of Ligula, but as Abothrium crassum.

Taenia spec. TOSH (99). 1905. "One larva was observed", 40 writes TOSH in his report on the parasites of the Tweed salmon. Of course we cannot draw any conclusions whatsoever from this note. If it was really a Taenia, the report is interesting inasmuch as it indicates that apart from Bothriocephala, Taenia can also parasitize Salmo salar.

Cysticercus spec. GIEBEL (28). 1866. A very questionable species which does not lend itself to any interpretation.

Bothriocephalus imperfectus cysticus CREPLIN (16). 1848. This form does not offer any clues for discussion. From the term "cysticus" one might think of a Bothriocephalus larva found encapsulated in one of the organs.

Bothriocephalus spec. 1894. WARD (103) reports that the parasite collection by HASSALL contains a bothriocephalid species found in Salmo salar in England. Morphological details are missing.

Bothriocephalid larvae ZSCHOKKE. 1889, 1891, 1896.

In his extensive parasitic material collected in the years 1888 to 1890, ZSCHOKKE found a large number of larval forms; in a publication in 1890 he reported on their shapes and on their relations towards each other and to other, similar, already known forms (111). In his third publication on salmon parasites (112), we find additions to the above paper and its systematic classification. One species, Bothriocephalus spec. I 1890, was recognized as Bothriocephalus osmeri v. LINST. The others are referred to in literature as Bothriocephalus spec. I 1891, Bothriocephalus spec. II 1891 and Bothriocephalus spec. III 1891.

In 1896, the same author (114) reports again on several bothriocephalid larvae which he had found <sup>in</sup> salmon from the North Sea, from Holland and from the Middle Rhine. He does not mention their 41 systematic classification, their size and shape.

Tetrabothrium minimum (v. LINST). 1888. Until that year, this cestode larva was found in a few specimens only, and exclusively in Salmo salar. In 1888, Von LINSTOW (52) named it, but it seems to have been known even earlier, for in 1863 McINTOSH (64) mentions a gregariniform creature which he found frequently in the pyloric appendages of salmon intestines. He describes them and expresses the view that the animal might be a developmental stage of another parasite. From the description and the drawings a

certain resemblance to Tetrabothrium minimum does become apparent. An identification, already assumed by WARD (103), may perhaps be possible.

In 1905, TOSH (99) found another Tetrabothrium in a salmon from the River Tweed, also in the pyloric appendages, but he does not describe or depict it.

Tetrabothrium spec. TOSH. 1905. TOSH (99) calls the parasite which he found free-swimming in the rectum of a Tweed salmon, "probably more advanced forms of the last species", the "last species" being Tetrabothrium minimum v. LINST. Again no detailed description.

Tetrabothrium nov. spec. (larva). In the rectum of a Lower Rhine salmon which I examined in June 1912, I found a small, yellowish-white body of oval-heart-shaped contours.

The maximum length is 1,368 mm, the maximum width 1,113 mm. The anterior margin is deeply indented. This indentation is spherical 0.252 mm long. It continues into the body as a canal which widens sac-like at the base, approximately in the centre of the animal. The entrance of this indentation bears two strange tips of epidermal origin on either side. They are approximately 0.0155-0.0186 mm long. I cannot explain the physiological function of these structures.

This larva completely lacks any hairs or scales as I observed them 42  
on the bothriocephalid larvae from Oncorhynchus nerca (Kamtchatka)  
(116).

For further details and better understanding, reference  
should be made to Fig.5.

Opposite the indentation lies another shallow indentation,  
the excretory pore. The 4 excretory vessels which unite in front  
of the pore to a small vesicle, open into it. Of the 4 vessels,  
2 are particularly well developed; this was even more distinctly  
visible on transverse sections made of the parasites at a later date.

Inside, the larva is largely filled with parenchymatous tissue  
in which comparatively large, oval calcareous bodies lie dispersed.  
Then we find, practically in the centre of the body and on the  
inner end of the above-mentioned canal, the bothria and the rostellum.  
A narrow space is visible between this centrally located scolex  
complex and the above-mentioned tissue; it surrounds the scolex with  
its bothria like a shell.

The 4 large, auricle-shaped, multi-lobed bothria are  
located on the lateral walls of the above-described, bottle-shaped  
canal, with their concave surfaces turned towards the hollow space.  
The dorsal and ventral bothria are close to each other, while  
the left and the right one are located at a distance to each other.  
Inside these sucking surfaces the rostellum projects into the canal;

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on its tip it bears a fifth, small sucker, as I could ascertain from the transverse sections through the animal. It has no hooks.

Systematically, this peculiar cestode larva may be assigned to the group of Tetrabothria. It is presumably the developmental stage of one of the family of Ichthyotaeniida. It cannot be compared with Tetrabothrium minimum v. LINST.

Tetrarhynchus spec. Mc. INTOSH. 1863. McINTOSH (64) found the scolex of a Tetrarhynchus in the rectum of a salmon. Very little information can be derived from his drawing and description.

In my material, I found small bodies of similar shape and size which, as I will show further below, mostly proved to be developmental stages of Tetrarhynchus paleaceus RUD. If such parasites are crushed, one finds not only calcareous bodies (= "oval bodies or cells, pale and translucent", as McINTOSH describes them), but also parts of the scolex such as proboscis, proboscis sheaths and proboscis clubs. The Scottish scientists also saw such remains. It is therefore well possible that McINTOSH was dealing with developmental stages of Tetrarhynchus paleaceus. 43

Tetrarhynchus spec. ZSCHOKKE 1896. Without detailed description ZSCHOKKE (114) reports that he found a Tetrarhynchus

species in a North Sea salmon which he examined for parasites in 1896.

Tetrarhynchus rugosus BAIRD (3).1853. For the sake of completeness, this parasite shall be mentioned here. TOSH (99) identified it as Coenomorphus grossus (RUD.), but his definition of the host - "of a salmon" - is too inaccurate to be taken for Salmo salar with certainty. He might mean Salmo trutta.

The following, partly well-known and widely distributed species, which, however, are rare in Salmo salar, also belong to the group of the purely marine forms:

Tetrarhynchus paleaceus RUD. Small, yellowish-white, bodies of the size of a pin-head were occasionally found encysted or deposited in the esophageal or intestinal wall or between the pyloric appendages. Inside these bodies lay those parasitic larvae, enclosed in capsules of connective tissue, which are known as developmental stages of Tetrarhynchus paleaceus. ZSCHOKKE (112), too, found such structures of similar shape, size and number in Salmo salar and described them.

As I explained above, McINTOSH (64) was most likely dealing with the same parasites without recognizing them as Tetrarhynchus paleaceus.

The larva as well as the mature worm are purely marine parasites which, according to ZSCHOKKE (113) parasitize Scyllium stellare.

44

## Marine fish:

<u>Selachei:</u>	12	encapsulated in	)	Mediterranean,
		body cavity; free	)	more seldom
		in the intestine	)	in Atlantic
<u>Teleostei:</u>			)	Ocean; North
<u>Acanthopterygii</u>	15	" " "	)	Sea
<u>Anacanthini</u>	10	" " "	)	
<u>Physostomi</u>	3	" " "	)	
<u>Plectognathi</u>	1	" " "	)	

## Migratory fish:

Salmo salar

Rhine, Tay?

Tetrarhynchus quadrirostris (GZE.). This parasite is fairly common in Salmo salar. It lies encapsulated between the pyloric appendages, in the peritoneum, at the outer wall of the intestine, more rarely is it found free in the body cavity. Very rarely it is encountered on the outer surfaces of liver and spleen. The capsules are mostly elongate-oval and yellow to white. Only once did I find a specimen of Tetrarhynchus free in the body cavity, with its probosces attached to the intestinal wall.

As the parasite is known and has already been described, I need not give a detailed morphological description here. The specimens I found were between 2.5 and 6 mm long. For all other details, reference should be made to the description and drawing

in the publication on parasites of Salmonidae from Kamtchatka (116).

On the basis of my various finds from Rhine, Weser and Norwegian salmon which were all different developmental stages of Tetrarhynchus, I can confirm TOSH's (99) opinion that Tetrarhynchus quadrirostris (GZE.), Tetrarhynchus appendiculatus RUD., Tetrarhynchus megabothrius RUD. and Tetrarhynchus macrobothrius v. SIEB are synonymous species.

If we include all these synonyms, Tetrarhynchus quadrirostris parasitizes many marine fish. It is also reported to have been found in representatives of various other marine animals, as the following list of hosts shows: 45

Marine fish:

<u>Coryphaena equisetis</u>	Body cavity & intestine	)
<u>Coryphaena hippuris</u>	" "	} Mediterra- nean. At- lantic Ocean
<u>Halichelys atra</u>	" "	
<u>Scomber pelamys</u>	" "	
<u>Scomber scomber</u>	" "	
<u>Scomber spec.</u>	" "	
<u>Lampris guttatus</u>	" "	

Migratory fish:

<u>Salmo salar</u>	Body cavity	Rhine, Tay Tweed, Elbe, Weser
<u>Oncorhynchus tshawytscha</u>	"	Easterñ Kamtchatka

Cephalopoda:

<u>Loligo spec.</u>	"	} Mediterra- nean
<u>Sepia officinalis</u>	"	

Cheloniidae:

<u>Chelonia mydas</u>	"
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Coenomorphus grossus (RUD.). Another cestode larva seems to occur as frequently in Salmo salar as Tetrarhynchus quadrirostris (GZE.), namely Coenomorphus grossus (RUD.) which, being a purely marine <sup>parasite</sup> animal, occurs only in marine fish, with the exception of 3 migratory fish, as can be seen from the following list:

## Marine fish:

<u>Selachii:</u>	10	Body cavity; free in the intestine	} Atlantic Ocean; Mediterranean
<u>Teleostei:</u>			
<u>Acanthopterygii</u>	10	Body cavity	}
<u>Anacanthini:</u>	4	" "	

## Migratory fish:

<u>Salmo salar</u>	Body cavity	Rhine, Scotland, Ireland, Elbe?
<u>Oncorhynchus tshawytscha</u>	"	Eastern Kamtchatka
<u>Salmo trutta</u>	"	Scotland, Ireland

With regard to its relationship to other worms, this parasite occupies a special position in the literature on parasites. In 1838, DRUMMOND (19) found 2 larval forms (in Irish salmon) which he described in detail and depicted. He identified one form as Tetrarhynchus grossus RUD., while he interpreted the other one as a new species and called it Tetrarhynchus solidus DRUMM. This separation continued until 1891 when ZSCHOKKE (112) combined the two species, pointing out that the characteristics which might separate the two forms "are so negligible and inconstant that a separation seems hardly justifiable".

TOSH (99) then took a decisive step and combined the two

species under the name Tetrarhynchus grossus RUD. on the basis of reliable material from the Tweed salmon which he himself had collected. LÜHE (62) introduced the generic name Coenomorphus (grossus) instead of Tetrarhynchus (grossus).

I found the parasite several times in the body cavity on the intestine, on the peritoneum or also between the pyloric appendages in forms which resembled partly Tetrarhynchus grossus RUD., partly Tetrarhynchus solidus DRUMM. I fully agree with TOSH's (99) view that the species introduced by DRUMMOND under the name Tetrarhynchus solidus must be regarded as the <sup>obsolete name for</sup> ~~extinct form of~~ Tetrarhynchus grossus RUD. and must therefore be combined with the latter. The parasites grow to ~~an~~ enormous larvae in the body cavity of Salmo salar, but die after some time and are covered by the connective tissue of the body cavity with a tough capsule. In these capsules the former larvae are found in various positions - straight, bent or involuted. If we open the capsules, we find calcareous concretions and remains of the parasite inside.

I have nothing to add to the descriptions by DRUMMOND (19), BELLINGHAM (8), ZSCHOKKE (112) and TOSH (99). The biggest specimen was 30 mm long and had a maximum width of 8 mm. The dead forms were always smaller: 18-25 mm long.

Coenomorphus grossus was found in Salmo salar in Ireland, in the Tweed, the Rhine and the Weser. FRITSCH (24) presumably also

found it in the Elbe salmon, for Fig.49c in his report on the Elbe salmon depicts a parasite the shape of which is much more similar to the figures by TOSH and DRUMMOND of Coenomorphus grossus than to Figs. 49a and 49b depicting Tetrarhynchus quadrirostris. A comparison of the dimensions of Figs. 49a and 49b and Fig.49c also indicates that Fig.49c cannot be Tetrarhynchus quadrirostris, but rather Coenomorphus grossus. FRITSCH himself puts a question mark behind the name Tetrarhynchus macrobothrium - the term he used for the larval forms he depicted and described -, which shows that he himself was not quite certain whether all specimens were really the same. He states furthermore that he had found some larvae encapsulated in the intestinal wall and in the liver, some free in the body cavity. The first locality agrees with Tetrarhynchus quadrirostris, but not with Coenomorphus grossus. The second locality is the right one for the large larval form.

Therefore all these findings speak in favour of the view that FRITSCH was dealing also with Coenomorphus grossus from the Elbe salmon, but erroneously classified it as an advanced stage of Tetrarhynchus quadrirostris.

### β. Marine-potamophilous forms:

Tetrarhynchus erinaceus v.BEN. Twice in the Rhine area - once in the Upper Rhine, the other time in the Moselle -

I found, encapsulated in the esophageal wall, the larval form of Tetrarhynchus erinaceus described and depicted by VAN BENEDEEN (9). The same species in the same stage was also found once in a Weser salmon at the same place in the fish body.

The 4 specimens are very similar to the first developmental stages depicted by VAULLEGEARD (100). I could not find any more advanced forms. All cysts had a diameter of approximately 0.882 - 1.026 mm.

From the small number and the rare occurrence of the parasite in salmon (for the first time) it may be concluded that infection was accidental. This seems to be confirmed by the list of hosts, too, for the majority of marine fish which are hosts and intermediate hosts belong to the Selachii. The parasite was found only once in fresh waters, and only Anguilla vulgaris was known among migratory fish to be parasitized by it.

Marine fish:			48
<u>Selachii:</u>	10	mature in the intestine	) Mediterranean, Atlantic Ocean.
<u>Teleostei:</u>			) North Sea.
<u>Acanthopterygii:</u>	8	" " also	) North America (east coast)
<u>Anacanthini:</u>	4	" " encapsulated in body cavity	)
Migratory fish:			
<u>Salmo salar</u>		encapsulated in esophageal wall	Rhine North America
<u>Anguilla vulgaris</u>		" "	

## Freshwater fish:

Lota vulgaris encapsulated in body cavity Lake Geneva

ZSCHOKKE (115) has supplied us with a detailed faunistic and geographical report on Tetrarhynchus erinaceus. He discussed the very unusual occurrence in Lota vulgaris in great detail and reflected on the various possibilities of infection.

(= Scolex polymorphus RUD.)  
Scolex pleuronectis MÜLL. This parasite/is also predominantly marine, as the following list of hosts may show:

## Marine fish:

More than 150 species      Mediterranean, Atlantic Ocean, etc. etc.

## Migratory fish:

<u>Salmo salar</u>	Elbe, North Sea, Rhine
<u>Osmerus eperlanus</u>	North America (Atlantic coast)
<u>Petromyzon fluviatilis</u>	Germany
<u>Anguilla vulgaris</u>	North America (Atlantic coast)
<u>Alosa vulgaris</u>	?

## Freshwater fish:

<u>Cottus gobio</u>	Tiber
<u>Perca fluviatilis</u>	?
<u>Esox lucius</u>	France
<u>Salmo salar jun.</u>	Elbe

## Ctenophora:

Cydippe spec. Mnemia norwegica.

## Cephalopoda:

Octopus vulgaris, Eledone moschata, Loligo vulgaris,  
Loligo sagittata, Sepia officinalis.

## Crustacea:

Pagurus bernhardus, Carcinus maenas.

In Rhine salmon, I found Scolex pleuronectis only once in 49 the appendix region of the intestine, together with several specimens of Abothrium crassum. As the larva is sufficiently known from previous reports, and my observations agree completely with those by RUDOLPHI (87), DIESING (18), MONTICELLI (71) and other authors, I need not describe it here.

LÜHE (62) is mistaken when he states that Scolex pleuronectis had already been found in Salmo salar from the Rhine; this is not a fact. ZSCHOKKE (114) found the parasite once in a North Sea salmon. I do not know of any other finds of Scolex pleuronectis in Rhine salmon; therefore, my find appears to be the first one of its kind.

This cestode has been known from the Elbe salmon since 1893; according to FRITSCH (24), it occurs frequently in that salmon all the year round. It has also been found in young salmon of the Elbe river which fact induced ZSCHOKKE to assume (115) that "Calliebothrium (C. filicelle), the adult chain form of Scolex polymorphus, is occasionally introduced into the rivers".

Schistocephalus gasterostei (FABR.). ZSCHOKKE (112) found this parasite in the stomach of a Baltic Sea salmon (not in a Rhine salmon, as the list of parasites erroneously indicates).

The parasite is almost purely potamophilous, as the list of hosts and localities shows:

Larva in:

Marine fish:

Cottus scorpius Esophagus ?

Migratory fish:

Salmo salar Stomach Baltic Sea

Freshwater fish:

<u>Cottus poecilopus</u>	Esophagus	?
<u>Gasterosteus aculeatus</u>	Body cavity	East Prussia, Normandy, Greenland
<u>Gasterosteus pungitius</u>	"	Sweden
<u>Gasterosteus spec.</u>	"	Lake Vyazero (Russia)

Amphibia:

Rana esculenta Intestine 50  
Pillau (East Prussia)

Mammals:

<u>Phoca vitulina</u>	Rectum	Baltic Sea
<u>Phoca foedita</u>	"	"
<u>Fetis domestica</u>	?	(acc.to CREPLIN region of Baltic Sea?)

Mature in:

Numerous aquatic birds

Its geographical distribution is limited almost exclusively to the Baltic Sea and the surrounding coastal areas.

Trianenophorus nodulosus (PALL.). This parasite was also found by ZSCHOKKE (112) encapsulated in the liver of a Baltic Sea salmon.

It parasitizes mainly freshwater fish as hosts and intermediate

hosts. It has the following hosts:

Marine fish:

<u>Belone acus.</u>	Intestine	Italy
<u>Syngnatus hippocampus</u>	"	"
<u>Pleuronectes flesus</u>	Encapsulated	Baltic Sea
<u>Zoarces viviparus</u>	Encapsulated in liver	"

Migratory fish:

<u>Salmo salar</u>	Encapsulated in liver	Baltic Sea
<u>Salmo trutta</u>	Encapsulated in muscles	?
<u>Anguilla vulgaris</u>	Intestine	?

Freshwater fish:

<u>Acanthopterygii:</u>	5 )	free in intestine )	
<u>Anacanthini:</u>	1 )	and encapsulated )	Central Europe
<u>Physostomi:</u>	23 )	in body cavity )	

Migratory fish are among both hosts and intermediate hosts; this may be one reason for the large distribution of this parasite. It is an interesting fact that the parasite seems to have become a regular inhabitant of the Baltic Sea so that marine and migratory fish alike can be infected there. Salmon, too, presumably acquired his Triaenophorus infection there. The parasite spends its life encapsulated in the liver of the salmon, dies there and forms concretions of a hardness similar to that of the concretions found by SCHNEIDER in Zoarces viviparus.

g. Purely potamophilous forms:

Abothrium crassum (BLOCH). The bothriocephalid form

Abothrium crassum (BLOCH) is well known to any parasitologist examining Salmo salar for parasites. Like Derogenes varicus in the stomach and Ascaris capsularia in the body cavity, this cestode can be expected almost with certainty in any salmon intestine. In most cases the scolex lies in one of the caeca while the chain of proglottids forms convoluted loops at the entrance of the intestine and often extends far into the small intestine with its loops. Frequently the number of parasites is so large that the worms form large clumps or complicated convolutions in the pyloric intestine. In the salmon of the Upper Rhine, entire worms or smaller or bigger parts consisting of several proglottids each are found occasionally in the terminal intestine. It seems as if the parasite left its host in fresh water. I shall return to this question and similar cases in another context further below.

On an average I found the parasite more frequently than ZSCHOKKE (112) - 58.23% of the examined salmon, that is more than half, were infected with it. The intensity of infection differed, it was greatest in salmon from the lower course of the river. The average number of parasites in one fish was 1-20, but in most cases the fish had only 1-2 specimens which were then very long. Only once were 52 cestodes collected from one salmon from the Lower Rhine; the maximum length of these cestodes, however, ~~did~~ hardly ever exceed 5 cm. Except in the above-mentioned case, I

never found degrees of infection as high as those observed in the Baltic Sea salmon by SCHNEIDER and in Rhine salmon by ZSCHOKKE, but I found sometimes giant specimens instead. Once I found in one single salmon from the Lower Rhine 4 bothriocephalids which were 70, 92, 95, and 97 cm long, respectively. The longest proglottid chain I ever found was also in a Rhine salmon; it was 120 cm long.

Here I would like to refer briefly to the large number of synonyms of Abothrium crassum (BLOCH). After intensive studies on parasites from Lake Geneva, ZSCHOKKE (108) solved the problem of the difference between Bothriocephalus proboscideus RUD. and Bothriocephalus infundibuliformis RUD. by recognizing them as synonymous forms. RIGGENBACH (86) showed that Bothriocephalus salmonis umbra KÖLLIKER and Bothriocephalus suecicus LÖNNB., which LÖNNBERG (57) had introduced as a variety probably caused by climatic conditions, are also identical with Abothrium crassum. LÜHE (59) considered the cestode, introduced by MONIEZ (69,70) as the representative of a new genus, Leuckartia nov.gen., also synonymous to Abothrium crassum. 52

The reason for this creation of new names for the same parasite, for these numerous confusions, is to a large part the changing and sometimes strange development of the scolex of the parasite.

I studied this question at some length on my extensive

material, and I would like to summarize the results in a few self-explanatory drawings.

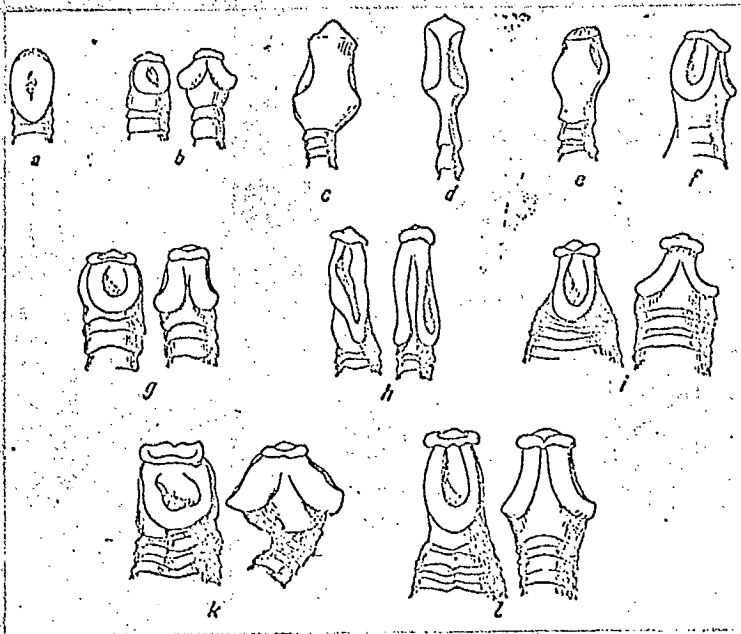


Fig.1.

Scolex forms of Abothrium crassum (BLOCH)

- a,c,f - according to OLSSON (1876)  
 d - according to ZSCHOKKE (1884)  
 e - according to FRITSCH (1894)  
 b,g,h,i,k,l - drawn from nature and preparations (1914-15)  
 (l = normal)

The development of Abothrium crassum has not yet been quite clarified. SCHNEIDER (90) found larval stages of this cestode in Salmo salar and in the two coastal fish Clupea harengus membras and Cyclopterus lumpus. These adolescent stages were not sexually differentiated and lay free in the intestine. The larval forms which ZSCHOKKE (108) found in various fish from Lake Geneva, cannot with certainty be classified as Abothrium crassum. 53

We know as little about the manner in which salmon gets infected with this parasite as about its development. We also do not know where and when. From the list of hosts we see that Abothrium crassum is a purely potamophilous parasite. Therefore,

infection can take place only in fresh water or possibly in the brackish water in the mouth of the river. I suspect that Salmo salar becomes infected with the parasite through feeding on small fish which carry the worm in some larval stage. The various species of stickleback would be above all concerned because they are known to be able to live equally well in fresh water, brackish water and salt water and they often carry this cestode.

In any case, this question of infection has yet to be answered. Perhaps we are closer to a solution than we expect, for SCHNEIDER (91) pointed out that Bothriotaenia rugosa is very similar to Bothriotaenia proboscidea and that the differences stressed by LÜHE (59) and RIGGENBACH (86) are negligible and not constant. In his opinion, the distinguishing characteristics might be "included in the range of variations of one species". If this were true and Abothrium rugosum could be combined with Abothrium crassum, the latter would naturally lose its exclusive potamophilous character. The list of hosts would <sup>have to</sup> be extended to include, in addition to the 8 migratory fish and 20 freshwater fish, 10 marine fish and 1 freshwater fish as hosts of Abothrium rugosum. From the parasitological viewpoint and in view of the mode of infection of Salmo salar, such a combination of the two species could almost be encouraged. I shall discuss this question once more in the faunistic-biological part.

Perhaps TOSH's (99) statement is already based on such a combination, for the reports that Abothrium crassum is the parasite of many marine fish, which would of course not apply if Abothrium crassum and Abothrium rugosum were different forms. 54

ZSCHOKKE's statement (115) on the occurrence of Abothrium rugosum in Salmo salar presumably is due to a mistake, at least there is not enough proof for the find. In any case, this case shows, too, how close we might have come towards a combination of Abothrium crassum and Abothrium rugosum.

Below, a list is given of fish infected by Abothrium crassum.

Marine fish (as intermediate hosts):

<u>Cyclopterus lumpus</u>	Intestine	Baltic Sea
<u>Clupea harengus membras</u>	"	"

Migratory fish:

<u>Salmo salar</u>	Pyloric appendages and intestine	Arctic Ocean, North and Baltic Seas, Atlantic Ocean (European and American coasts)
<u>Salmo trutta</u>	" "	Baltic Sea, Sweden, Scotland
<u>Salmo salar, var. nobilis</u>	" "	Murman Coast (White Sea)
<u>Salmo caspius</u>	" "	Kara-Bogaz-Gol (Caspian Sea)
<u>Oncorhynchus keta</u>	" "	Kamtchatka, Alaska
<u>Oncorhynchus nerka</u>	" "	" "
<u>Coregonus oxyrhynchus</u>	" "	Gulf of Bothnia
<u>Osmerus eperlanus</u>	" "	" "

Freshwater fish:

<u>Acanthopterygii:</u>	1	Pyloric appendages and intestine)	Russia, Scandinavia,
<u>Anacanthini:</u>	1	" "	Germany, Holland,
<u>Physostomi:</u>	18	" "	Belgium, France,
		)	Switzerland, Italy,
		)	North America

The above list also shows the wide range of geographical distribution. Abothrium crassum is found in practically all fresh waters of the Arctic and temperate zones of the northern hemisphere.

Before I conclude this chapter on the salmon cestodes, I would <sup>like</sup> to refer briefly to one parasitic species which for a long time was erroneously included in the list of salmon parasites and was removed from there only by WARD (103). The species is Bothriocephalus cordiceps LEIDY. It parasitizes Salmo mykiss where it lives as larva in the body cavity. As mature form it parasitizes aquatic birds. 55

Nemathelminthes:

(c) Nematodes: According to their origin, the salmon nematodes can be divided into the following groups:

α. Marine forms: 5 (3 of which parasitize the Rhine salmon)

β. Marine-potamophilous forms: 2 (2 of which parasitize the Rhine salmon.

γ. Potamophilous forms: 2 (none of which parasitize the Rhine salmon.

Of the 9 nematodes, 5 have been found in Rhine salmon. We see from the summary also that the Rhine salmon does not manifest

any purely potamophilous elements. The salmon of the Baltic Sea, the Weser, Tay and Tweed rivers carry in addition to marine species also potamophilous species which makes the life of these fish appear in a special light in biological respects.

α, Marine forms:

Ascaris adunca RUD. I found Ascaris adunca, a parasite usually occurring in marine fish only, in the esophagus, in the region of the pyloric appendages and occasionally also in the terminal intestine. The fish infected by this parasite (9 Lower Rhine and 3 Norwegian salmon) had many food remains in their entire digestive tract in addition to the parasite. Ascaris adunca presumably entered the intestine of the salmon with the food - small fish (herring, etc.).

Almost always, the number of Ascaris adunca in one salmon was small; only once I found 78 specimens in the stomach and intestine of one single fish from the Lower Rhine. In that case, however, the digestive tract was crammed with food remains, too.

With regard to outer appearance and structure of the organs, 56 I have nothing to add to the descriptions by RUDOLPHI (87), SCHNEIDER (89), and v.LINSTOW (51). Female specimens were always in the majority: among 100 parasites I found only 4 male ones.

The list of hosts is as follows:

Marine fish:

<u>Acanthopterygii</u> :	8	Stomach & intestine	)	Mediterranean,
<u>Anacanthini</u> :	7	" "	)	Atlantic Ocean,
			)	North and Baltic
			)	Seas. White Sea.
			)	South America
			)	(Ushuaia)

Migratory fish:

<u>Salmo salar</u>		Stomach and intestine		North and Baltic
				Seas. Rhine
<u>Osmerus eperlanus</u>	"	"		?
<u>Alosa vulgaris</u>	"	"		Rimini, Trieste
<u>Alosa finta</u>	"	"		" "
<u>Alosa sapidissima</u>	"	"		North America
<u>Anguilla vulgaris</u>	"	"		Gulf of Finland

A probable intermediate host is also an isopod, Idotea entomon, which is the staple food of many small marine fish.

Several specimens of Ascaris acuta RUD./this parasite were found by TOSH (99) in the stomach of Tweed salmon. From the list of hosts it appears to be rare, and in Salmo salar it is presumably an accidental guest.

Marine fish:

<u>Rhombus maximum</u>	Intestine	Padua
<u>Rhombus barbatus</u>	"	"
<u>Rhombus spec.</u>	"	Italy
<u>Platessa plana</u>	"	North America

Migratory fish:

<u>Salmo salar</u>	Intestine	Tweed
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We know nothing about the development of Ascaris acuta.

Ascaris clavata RUD. ZSCHOKKE (110,112) found this parasite 8 times in Rhine salmon, always encapsulated in the esophageal wall or in the peritoneum. Presumably, this migratory fish became infected with Ascaris clavata by feeding on gadids which are frequently parasitized by that nematode species. It is strange that the parasite was found to have encapsulated itself when sexually mature. Perhaps Salmo salar is not a suitable host for this nematode species so that it tries to protect itself in that manner. 57

Marine fish:

<u>Acanthopterygii</u> :	6	Intestine and stomach	) Atlantic Ocean, North and Baltic Seas, Arctic Ocean, Mediterranean.
<u>Anacanthini</u> :	16	" "	)
<u>Physostomi</u> :	4	" "	)

Migratory fish:

<u>Salmo salar</u>	encapsulated in body cavity, peritoneum, esophagus	Rhine, Elbe, Ireland
<u>Salmo trutta</u>	encapsulated in peritoneum, intestine	Ireland

Ascaris communis (DIES.). This parasite was found by ZSCHOKKE (112) in the body cavity of various Rhine salmon. The further development of this nematode larva is unknown.

Marine fish:

<u>Acanthopterygii</u> :	8	mostly encapsulated in body cavity	) Bering Sea, Arctic Ocean, Scandinavia,
<u>Anacanthini</u> :	7	" "	) Atlantic Ocean, North America

Migratory fish:

<u>Salmo salar</u>	mostly encapsulated in body cavity	Rhine
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Ascaris angulata RUD. ZSCHOKKE (112) found a mature worm of this nematode species in the esophagus of a Rhine salmon. From the locality it could be concluded that the parasite was trying to leave its host. Presumably, Ascaris angulata is as much an accidental guest of Salmo salar as Ascaris clavata. Usually the worm parasitizes mostly various Cottus species, as becomes clear from the list of hosts:

Marine fish:

<u>Cottus scorpius</u>	Intestine and stomach	White Sea
<u>Cottus quadricornis</u>	Body cavity	Baltic Sea
<u>Cottus bubalis</u>	Intestine	North America
<u>Lophius piscatorius</u>	"	Ireland

Migratory fish:

<u>Salmo salar</u>	Esophagus (gullet)	Rhine
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β. Marine-potamophilous forms:

Ascaris capsularia RUD. This nematode larva which has been known for the longest time, almost always occurs in Salmo salar. Again and again this undeveloped nematode is found in various organs of the body cavity, mostly enclosed in a shining white, sometimes slightly iridescent capsule. It is to be found everywhere - in the peritoneum, the liver and the spleen, across

the entire outer wall of the intestine, between the pyloric appendages.

Of the 170 examined Rhine salmon, 140, that is 83.3%, were infected with a total of 554 specimens. Often there were only few specimens in one fish, and then again many, but 17 was the maximum. Of the salmon from other rivers which I had an opportunity to examine, always more than half, often all of them were infected. In ZSCHOKKE's (112) case, 76.5%, that is slightly less than for my salmon, of the material were infected, but the number of parasites found in one fish was considerably higher. He reports 20-30 specimens in one fish.

The view that Ascaris capsularia can, if necessary, undergo a free-living stage between the larval and the mature stages, gave rise to many studies. RUDOLPHI (87), WEDL (106), also ZSCHOKKE (112), and most recently DEWITZ (17) demonstrated by tests that the parasite can survive in water for 2-3 weeks. My tests in this direction yielded similar results. Therefore a free-living stage is not out of the question. The parasite is able to leave the dead host (which, according to LEIDY, 47, is always the case) or an unsuitable host to find probably better living conditions in another host.

I have nothing to add to the reports by RUDOLPHI (87), DUHARDIN (20), etc. on the parasites I found. I would only like to relate very few observations at this opportunity.

Dimensions vary greatly. I found specimens of lengths between 15-35 mm. The disc-shaped capsules contain the animal involuted in one plane, the anterior end always towards the edge, the posterior end in the centre of the disc. This observation agrees with the one made by McINTOSH (64). There was not one among the many hundreds of ascarids which was involuted in a different manner. The diameter of the capsule of connective tissue, flattened on both sides, is approximately 10 mm. With a slight tug the parasite can be pulled out of its capsule which surrounds its entire length like a tube, and then it rolls itself up again immediately. When placed in water, it moves with vivid, serpent-like motions.

Ascaris capsularia has a very wide range of distribution of all salmon parasites in every respect, in fact, the widest range/after ~~that of~~ Scolex pleuronectis.

Marine fish:

<u>Selachii:</u>	3	mostly encapsu-	)	Mediterranean,
<u>Teleostei:</u>		lated in and on	)	Atlantic Ocean,
<u>Acanthopterygii:</u>	33	the various organs	)	North and Baltic
<u>Pharyngognathi:</u>	3	of the body cavity	)	Seas, North
<u>Anacanthini:</u>	40	rarely in the	)	America (Atlantic
<u>Physostomi:</u>	9	intestine	)	coast). South
<u>Lophobranchi:</u>	2		)	America (Chile)

Migratory fish:

<u>Salmo salar:</u>	mostly encapsulated	Rhine, Elbe, Norway, etc.
<u>Oncorhynchus keta</u>	in and on the various	)
<u>Oncorhynchus tschawytscha</u>	organs of the body	)
<u>Oncorhynchus nerka</u>	cavity; rarely in the	) eastern
<u>Alosa vulgaris</u>	intestine	) Kamtchatka
<u>Alosa sapidissima</u>		) Warnemünde (Baltic)
<u>Anguilla vulgaris</u>		) North America
<u>Acipenser sturio</u>		) " Italy, Adria

## Migratory fish (continued):

Acipenser Guldenstädtii free in intestine Caspian Sea

## Freshwater fish:

Esox lucius

Muscles

?

Thymallus vulgaris

Body cavity

Wurttemberg

Lota vulgaris

"

Lake Geneva

Also in Diomedea spec. (Kamtchatka) and in Phocaena communis

ZSCHOKKE (115) has already discussed the occurrence of this parasite in the purely potamophilous fish Esox lucius, Thymallus vulgaris and Lota vulgaris.

From all these observations and examinations and from the above list we see that Ascaris capsularia is a widely distributed, very common fish parasite. Further studies will perhaps clarify the life cycle of this ascarid larva. They will also show whether STOSSICH is correct if he says that presumably capsule-forming larvae of various ascarids are classified under Ascaris capsularia. 60 If this is the case, the list of intermediate hosts and the geographical distribution of Ascaris capsularia will be considerably reduced.

Cucullanus elegans ZED. There is little proof for CREPLIN's report (17) that Cucullanus elegans, a nematode purely potamophilous with one very doubtful exception, was found in the intestine of Salmo salar. Unfortunately, CREPLIN did not give a morphological description of the worm he found or details on

the origin of the infected salmon. Perhaps it was a Baltic Sea salmon.

DUJARDIN (20) found the only marine host, Labrax lupus, infected with Cucullanus elegans. The author does not say where the fish came from. Perhaps it was a Labrax from a fish-pond, as this species is often raised and bred in ponds.

Cyclops quadricornis and Asellus aquaticus have long been known as intermediate hosts.

The following list may inform on the hosts established until then and on the geographical distribution of the parasite:

Marine fish:

<u>Labrax lupus</u>	Intestine	Adria?
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Migratory fish:

<u>Coregonus oxyrhynchus</u>	Intestine	Greifswald?
<u>Osmerus eperlanus</u>	"	" ?
<u>Salmo salar</u>	"	" ?
<u>Salmo trutta</u>	"	Görz, Trieste
<u>Anguilla vulgaris</u>	"	Switzerland, Bohemia, East Prussia

Freshwater fish:

<u>Pharyngognathi:</u>	7	Intestine, stomach	)
<u>Anacanthini:</u>	1	" "	) Europe
<u>Physostomi:</u>	10	" "	)

§. Purely potamophilous forms:

Ascaris aculeati v.LINST. ZSCHOKKE (112) found this rare parasite only three times in Baltic Sea salmon, I found it once in a Weser salmon, unfortunately in a highly damaged condition; 61 the parasite showed only the characteristics required for classification and identification. Von LINSTOW (51) found Ascaris aculeati for the first time in 1884 in Hameln in Gasterosteus aculeatus, and has described also embryonic and larval stages of the parasite. The appearance of my specimen which I found coiled up in a capsule in the esophageal wall, agrees with that description.

We can only speculate on the way in which the salmon was infected. It might have become infected directly in fresh water; on the other hand, Gasterosteus aculeatus perhaps plays the role of intermediate host and carrier as in the case of Abothrium crassum.

Ascaris obtusocaudata RUD.TOSH (99) found this parasite in a Tweed salmon. It is a typical salmonid parasite of purely potamophilous character. Its hosts are the following:

Migratory fish:

<u>Salmo salar</u>	Stomach	Tweed
<u>Salmo trutta</u>	Stomach, intestine	?
<u>Coregonus oxyrhynchus</u>	"	?

## Freshwater fish:

<u>Salmo lacustris</u>	Intestine	Lake of Lucerne
<u>Salmo fario</u>	Stomach, in-	
	testine	Rennes, Ireland
<u>Coregonus Wartmannii</u>	" "	?

Unidentifiable nematodes. In the course of their parasitological studies of salmon, McINTOSH (64), but also ZSCHOKKE (110,112), found nematodes which could not be identified; they were either damaged, stunted specimens or completely undeveloped individuals. I, too, found often nematode-like animals the systematic position of which I was unable to establish. Very frequently I found strangely stunted structures between the pyloric appendages or in the peritoneum. In most cases they were shaped like a club, and often covered with a sheath. After removal of the cover of connective tissue, a hard, granular mass remained. I examined these structures more thoroughly and came to the conclusion that they were degenerated and dead nematodes, presumably Ascaris capsularia, 62 which had been ~~so~~ strangely transformed by the calcareous concretions of the tissues surrounding them. McINTOSH had come to a similar conclusion in his report (64).

In addition to these calcareous concretions, nematodes enclosed in cysts in the esophageal wall were found which were as transparent as glass, had no definite outer or inner characteristics, were only a few millimetres long, and could not be identified. They

may have been embryonic stages of some nematodes.

The following authors, too, mentioned unidentifiable, encapsulated nematodes in Salmo salar:

In 1896, ZSCHOKKE (114) reports two ascarid species, Ascaris spec.I and Ascaris spec.II, without detailed identification and description.

In 1901, LINTON (56) briefly describes a nematode species from Salmo salar and also depicts it. We can only speculate on what species it belonged to; perhaps it was Ascaris capsularia, as already pointed out by the author.

(d) Acanthocephala: The parasitic fauna of the salmon includes very few Acanthocephala, both numerically and by species. So far 8 species are known, not counting the questionable and inaccurately described forms mentioned occasionally in literature. By origin, they divide into the following 3 groups like the rest of the salmon parasites:

α. Marine forms: 2 (2 of which parasitize the Rhine salmon.

β. Marine-potamophilous forms: 5 (2 of which parasitize the Rhine salmon.

γ. Potamophilous forms: 1 (1 of which parasitizes the Rhine salmon.

Of the 5 marine-potamophilous parasites, 4 infect predominantly freshwater fish and only one, Echinorhynchus gadi, parasitizes mainly marine fish. Thus the acanthocephalan fauna of the salmon is predominantly potamophilous and only to a small extent marine.

α. Marine forms:

63

Neorhynchus agilis (RUD.)<sup>1</sup>. ZSCHOKKE (112,114) found this species very rarely in the gullet and the esophagus of North Sea and Rhine salmon. It is purely marine, as the following list of hosts shows:

Marine fish:

<u>Selachii:</u>	1	Intestine	)	Mediterranean, North
<u>Teleostei:</u>		"	)	America (Woodshole)
<u>Acanthopterygii:</u>	6	"	)	
<u>Physostomi:</u>	1	"	)	

Migratory fish:

<u>Salmo salar</u>	Esophagus and gullet	Rhine, North Sea
<u>Anguilla vulgaris</u>	Intestine	North America

The geographical distribution of Neorhynchus agilis is interesting. The parasite seems to live mainly in the Mediterranean and on the Atlantic coast of North America. Only migratory fish carry

<sup>1</sup> The generic name Neorhynchus is to be replaced by Eorhynchus, according to VAN CLEAVE (Eorhynchus a proposed name for Neorhynchus HAM. Jour. of Parasit. No. 1, 1914), since the first name is already being used. I have refrained from discussing this point here in detail.

it further north. It has never been observed in the Arctic zone and in the Baltic Sea.

Echinorhynchus heteracanthis nov. spec. In November 1912, I found a strange acanthocephalan form between the pyloric appendages of a Rhine salmon caught above Basle. The parasite had attached itself to the connective tissue of the anterior appendage with its protruding proboscis, its body extended free into the body cavity. It had a yellowish-white colour.

The only specimen I found is female according to my findings. The parasite is 12 mm long from the sheath of the proboscis to the posterior end, its maximum width of 0.972 mm is in the anterior part of the body.

A short, club-shaped proboscis is followed by an even shorter neck defined from the proboscis by a weakly indicated furrow. A clearly defined furrow, on the other hand, separates the neck from the body. The latter is divided into two completely different parts which I would like to call anterior and posterior part of the body (see Fig.2 in the text). The anterior part is round at its ends adjoining the neck, and it is shaped like a truncated cone. Towards the rear it widens constantly and gradually becomes a bulge which, on account of its shape, I would like to call ring-like bulge. The anterior part of the body bears spines and contains

the sheath of the proboscis and the lemnisci. The round posterior part of the body follows the anterior part directly, without constriction, but at its origin it is after all a little narrower than the ring-like bulge of the anterior part. It increases gradually in circumference from front to rear and terminates shortly truncate. It contains the genital organs, in my case the female ones.

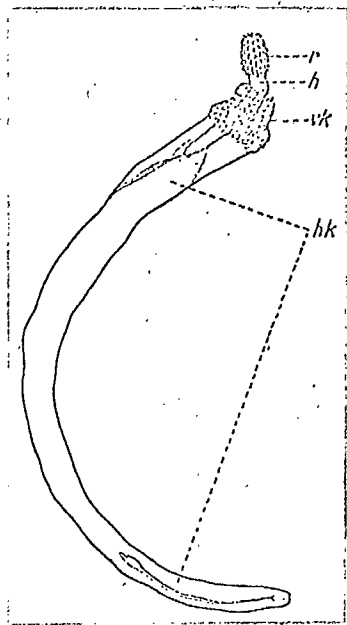


Fig.2.

Echinorhynchus heteracanthis nov.spec.

r - proboscis, h - neck, vk - anterior part,  
hk - posterior part of the body

From the tip to the neck furrow, the proboscis is 0.738 mm long, its maximum width, slightly behind the middle, is 0.486 mm. It is armed with 18 longitudinal rows of 8 hooks each. The 144 hooks occupy the usual quincunx. They differ in size and shape so that we can distinguish 3 different types. The first hooks of each row are slender and pointed and stand <sup>off</sup> slightly from the body. Their roots are approximately as long as the hooks themselves.

These hooks are followed by the longest and strongest hooks of each row. The latter originate with a broad base from roots which have the same width, and they are approximately 0.1085 mm long. The root is 0.1178 mm long and not deeply inserted into the skin; the roots is therefore slightly longer than the hook itself. The hooks are strongly curved so that the tips stand parallel to the surface of the body. These strong hooks are followed by hooks which could be compared to spines: they have no roots, are hardly curved and stand off from the body. From front to rear their length also increases, 65 the second last hook being the longest, but also the most slender hook of all; it is 0.0992 mm long. The last hooks of each row are again shorter (0.0713 mm); they also disturb somewhat the normal quincuncial arrangement because they stand more or less on one line.

I did not find any canals inside the hooks. Rarely the tips are curved outward. They are armed in the same manner in the same zone in all longitudinal rows so that we cannot distinguish between ventral and dorsal surface.

The proboscis is followed by the short, unarmed, conical neck. It is 0.306 mm long.

The anterior part of the body is 0.810 mm long, its maximum width at the ring-like bulge is 0.972 mm. The anterior part bears strange hooks which again differ in size and shape from each other. They are completely imbedded into the body skin which they raise

with them, creating a structure resembling the broad tip of a lance.

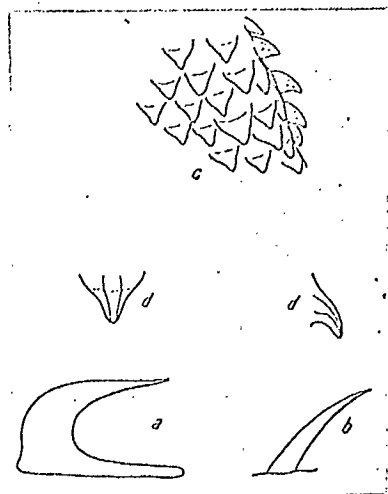


Fig.3.

Echinorhynchus heteracanthis HEITZ

Types of hooks: a,b - of the proboscis  
c,d - of the anterior part  
of the body

The shape of the skin lobes differs widely. In the first row the lobes are short and bottle-shaped; farther towards the rear we find lobes with approximately the shape of an equilateral triangle. Particularly those located on the ring-like bulge resemble scales of a fir cone. In the front these lobes are at a greater distance from each other, while towards the rear they approach each other so closely that the pattern looks like an accumulation of regular rhombi.

I tried to count the number of transverse rows and the number of hooks or lobes in one row, but found it very difficult on account of the strong contraction of the anterior part of the body. There are approximately 22 transverse rows the last 8 of which are located on the ring-like bulge. The anterior rows have between 26 and 32, the rows on the bulge approximately 72-80 hooks. 66

The hooks themselves are rather thick, pointedly triangular and slightly curved inward, with a blunt tip. The anterior hooks are more slender than the posterior ones. Also, the anterior hooks are slightly sinuated towards the inner side near the base. They are 0.0310 mm long. They do not have roots. The posterior hooks do not have roots, either, and are shaped like broad clubs and only slightly curved. They are 0.0434 mm long.

The posterior end of the anterior part of the body does not have any more hooks, neither ventrally nor dorsally. Similarly, there are no hooks at the end of the posterior part of the body, a sex characteristic which is often encountered in females of species with armed body.

The diameter of the round posterior part of the body changes; it decreases slowly from front to rear. Immediately behind the ring-like bulge it is 0.792 mm wide, in the middle 0.666 mm, and shortly before the end only 0.468 mm.

From the degree of development of all organs we see clearly that we are dealing with a larval stage, although far advanced. I will try to describe the animal as accurately as possible from the very transparent total preparation of the larva, so that it will be recognized in later studies and finds.

The thickness of the body covering of Echinorhynchus heteracanthis varies in different places. In general, it increases

from front to rear, and is greatest on either side of the vagina. The body does not show any girdling.

The lacunar system of the body consists of 2 longitudinal branches extending <sup>along</sup> across the entire body which are connected with each other by ring canals at a right angle to the body axis. The two longitudinal canals are connected with the two large, leaf-shaped, wrinkled lemnisci which lie on either side of the sheath of the proboscis. Their average length being 1.710 mm, they extend beyond the sheath of the proboscis. The latter is a muscular, double-walled sac. It is 1.566 mm long and has a maximum width of 0.414 mm. 67

Inserting in the inner wall of the neck, the sheath extends through the neck and the entire anterior part of the body, well into the posterior part of the body. The size of the sheath which consists of 2 strong, closely adjoining muscular cylinders, indicates that the entire proboscis can be retracted into it.

The unpaired Retractor receptaculi is a direct continuation of the Invaginator rostellii. It leaves the sheath through a crater-like opening of the outer muscular cylinder and extends obliquely towards the body wall as a thick, strong muscular bundle. Here it inserts by the individual fibre bundles assimilating into the longitudinal muscles of the body. The retractor is approximately 0.954 mm long.

The nervous system is characterized by the retinaculum

of which Echinorhynchus heteracanthis seems to possess only one. In spite of high magnifications and careful examinations I have not succeeded in finding a second retinaculum like in other acanthocephalans. 0.250 mm from the posterior end of the receptaculum the nervous bundle from the inside of the sheath penetrates the sheath muscles. This point of exit is marked by a slight elevation of the muscular walls where the muscle fibres surrounding the nervous bundle originate which together with the latter form the very strong retinaculum extending obliquely towards the body wall. It is 0.810 mm long. From the course of the nervous bundle inside the sheath it seems that the central nervous system lies in the middle or even farther towards the front in the sheath.

The posterior part of the body cavity contains the female genital organs which consist of three parts; they are fixed in their position by the ligamentum suspensorium. The bell of the uterus, the uterus and the vagina are clearly distinguishable.

On the ligament, approximately 0.306 mm from the bell of the uterus, the rudiments of a single, large ovarial disc are visible. It consists of different cell cluster complexes of varying sizes. Presumably these are the rudiments of the development of cell clusters from which the eggs are formed. I did not find any mature eggs anywhere in the genital organs.

The bell of the uterus is a complicated structure of several 68

large cells. The bell proper is very short and ring-shaped. It is followed by the base of the bell which consists of a few large cells. Above the lateral cells of the base we find the large, tubular bell pouches which are swollen to spherical shape at the ends and extend <sup>far</sup>/beyond the bell frontward. Inside they are hollow. Elongated, narrow cells of the base of the bell extend rearward and combine to form the two narrow oviducts which project into the anteriormost part of the uterus.

The uterus embraces the posterior part of the base of the bell, then tapers off quickly and extends toward the vagina as a thin canal with its lumina close together. The vagina consists of two unequal parts, namely the well developed sphincters and the glandular cells lining the vaginal canal. These cells surround the vagina in varying thickness which is greatest in front of and behind the sphincters. The entire structure which consists of 4 cells with their nuclei lying in the complex behind the constrictors, has a secretory function. The glandular cells are encircled by the 3 sphincters, the 2 inner ones one behind the other, and the third one surrounding these two. Together they form strong muscles presumably designed to squeeze the eggs from the vagina through the narrow canal. The vulva lies at the end of the posterior part of the body and is shaped like a pointed, funnel-shaped depression.

What, then, is the systematic status of this strangely built parasite and its relation to other marine and potamophilous fish acanthocephalans. We must not take the unilateral development of the nervous system, the retractor of the sheath of the proboscis and of the ovary to be specific or generic characters, for we cannot say from one specimen whether they are abnormal or constant developments.

On account of its armament and its shape, this new acanthocephalan from Salmo salar closely resembles Corynosoma (LÜHE),  
greatly  
but differs from that genus in various respects.

LÜHE (63) mentions three genera with hooks on the anterior 69  
part of the body: Polymorphus, Filicollis and Corynosoma. They differ, however, in structure, armament, inner organisation and in their hosts and intermediate hosts.

The new form shares the characteristic of the axial position of the proboscis with Polymorphus and Filicollis. Although in the specimen I examined the proboscis and the neck are slightly oblique, they are not bent dorsad or ventrad, the typical position for Corynosoma. Only a strong contraction of the muscles influences the position of the proboscis. The hooks, too, are different from those of Corynosoma and rather resemble those of Polymorphus and Filicollis. There are hooks only on the anterior part of the body, and there are none either on the dorsal or the ventral side of the

posterior part of the body.

The new species differs distinctly, however, from Polymorphus and Filicollis by the structure and the hooks of the proboscis, and by the shape of the entire body and its hooks. Also, the two other genera are found only in aquatic birds.

Let us compare this parasite with other fish acanthocephalans. It closely resembles Echinorhynchus serrani from Serranus artrarius, a form introduced by LINTON (55), also Echinorhynchus annulatus MOL. (68), but identification is impossible. Both those species have many more hooks on the proboscis. The anterior part of the body of Echinorhynchus annulatus (= bisulcatus) has a very similar structure, but its hooks are divided into 2 distinctly separate belts. The new acanthocephalan does have places with a considerably smaller number of hooks, but we cannot regard these places as a zone completely free of hooks.

In its outward appearance, with the exception of the hooks on the proboscis, Echinorhynchus serrani LINT. is very similar to this salmon parasite. Especially the hooks on the body as depicted by LINTON (55) in Fig.30 resemble those of the new species very closely.

Therefore the new salmon acanthocephalan cannot be assigned to either one of the groups mentioned, but occupies an intermediate position between the genera Filicollis or Polymorphus and Corynosoma.

As only one specimen of this new parasite is available which 70 makes it difficult to establish characteristics on which a new genus could be based, I have refrained from introducing a new genus and have called the new salmon parasite, a representative of the family of Acanthocephala, Echinorhynchus heteracanthis nov.spec.

Acanthocephale nov.gen., nov.spec., 1914. In the summer of 1914, I found an acanthocephalan in the parasitic material from the Russian Kamtchatka expedition which was very similar to the one described above. In the publication on the parasites of Salmonidae from Kamtchatka (116) it is referred to merely as Acanthocephale<sup>1</sup> nov.gen., nov.spec. from the intestine of Oncorhynchus nerca.

Already when I examined Echinorhynchus heteracanthis HEITZ from Salmo salar, I noticed the great similarity of the two forms; therefore I examined the acanthocephalan from Kamtchatka once more very thoroughly. As studies of fairly extensive comparative material of acanthocephalan species drew my attention to various errors made in previous descriptions of the worm, I would like to

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<sup>1</sup> Correction: In the publication by ZSCHOKKE and HEITZ "Endoparasites of Salmonidae from Kamtchatka" (Rev.Suisse Zool., Vol.22, 1914) the word Acanthocephale on page 231 was by mistake printed as if it were a new genus. This, however, is not the case. The name was merely used to signify that a new parasite had been found (nov.spec.) which belonged to Acanthocephala and presumably was at the same time a specimen of a new genus (nov.gen.).

report briefly on the new observations in connection with those old findings which are correct. I would also like to name this acanthocephalan, hitherto without name, which according to the kind written communication by Professor M. LÜHE is a representative of a new genus. However, I refrain from introducing a new genus for the same reasons as in the case of Echinorhynchus heteracanthis, and merely introduce a new species, but this species nova and Echinorhynchus heteracanthis are systematically very closely related.

Echinorhynchus caenoformis nov.spec. Length 6.7 mm; 71  
maximum width 0.756 mm. Short cylindrical proboscis which thickens slightly in the centre. The proboscis is 0.54 mm long and has a maximum width of 0.324 mm. 18 longitudinal rows of 6 hooks each of varying sizes and shapes. The 5 first hooks of each longitudinal row are large and strong. The root is 0.071 mm, the hook itself 0.083 mm long. The latter bends sharply rearward from the root, is straight and pointed. Very thin longitudinal canal inside the hook. The last hook of each longitudinal row is shorter than the other hooks (0.0558 mm), has no root, and stands off from the surface of the proboscis. Conical short neck.

The body consists of an anterior part which is pear-shaped and has hooks, and of a posterior part which is thinner and round and becomes thinner towards the rear. (In the two specimens, the

the anterior part of the body is shortened considerably by a strong contraction of the body muscles and is therefore swollen to such an extent that it extends beyond the posterior part, equally shrunk on account of the muscle contraction, like a hat). End of body rounded, without hooks. Hooks only on the anterior part of the body, no continuation beyond that, either ventrally or dorsally. The bases of the hooks on the anterior part of the body are thickened into clubs, and the hooks themselves are 0.456 mm<sup>long</sup> and are terminally blunt. The skin is raised by the tips of the hooks, forming scale-like structures. The sheath of the proboscis is a closed muscular sac with double walls. It inserts between proboscis and neck, and is 0.684 mm long. Retractor of the proboscis inserts on the top of the proboscis. There are two retractors for the sheath of the proboscis, they lie very close together and are parallel. Only one retinaculum visible.

The sac-like lemnisci are 0.864 mm<sup>long</sup> and extend beyond the sheath of the proboscis. 2 longitudinal canals extending <sup>along</sup> across the entire body are connected with each other by ring-shaped lateral branches and represent the excretory vessel. The ligamentum suspensorium (in the previous description erroneously called only muscular bundle) visible throughout the entire body. Genital organs not recognizable with the exception of the sphincters encircling the vagina. At the end lies the vulva (not excretory pore as the previous description has it).

It lives in the intestine.

Host: Oncorhynchus nerca.

Geographical locality: Kamtchatka.

$\beta$ . Marine-potamophilous forms:

Echinorhynchus gadi MÜLL. This acanthocephalan was found in Salmo salar from the Rhine, the Tweed and from East Prussia. The following list gives its other hosts and its geographical distribution.

Marine fish:

<u>Selachii:</u>	4	Intestine	)	Atlantic Ocean
<u>Teleostei:</u>			)	(European and American coasts).
<u>Acanthopterygii:</u>	18	"	)	North and Baltic Seas
<u>Anacanthini:</u>	31	"	)	
<u>Physostomi:</u>	4	"	)	
<u>Plectognati:</u>	2	"	)	

Migratory fish:

<u>Salmo salar</u>	Intestine	Baltic Sea, Rhine, Tweed
<u>Oncorhynchus nerca</u>	"	Eastern Kamtchatka
<u>Oncorhynchus keta</u>	"	"
<u>Anguilla vulgaris</u>	"	?
<u>Acipenser sturio</u>	"	Königsberg

Freshwater fish:

<u>Esox lucius</u>	Intestine	Baltic Sea (Gulf of Finland)
<u>Lota vulgaris</u>	"	Baltic Sea. Scandinavia
<u>Acerina cernua</u>	"	Baltic Sea (Gulf of Finland)
<u>Leuciscus idus.</u>	"	" "
<u>Silurus glanis</u>	"	? (according to MÜHLING)
<u>Coregonus lavaretus</u>	"	Ösel Island (Baltic Sea)

I shall not deal with the manner in which the 6 freshwater fish were infected with Echinorhynchus gadi, for the development of the parasite is still unknown. I would only like to point out that all infected freshwater fish came from the coastal waters and the brackish water regions of the Baltic Sea. Since the parasite is strongly marine, it is not surprising to find it in Salmo salar.

Echinorhynchus salmonis MÜLL. FRITSCH (24) found this acanthocephalan in Elbe salmon, TOSH (99) in Tweed salmon. It is predominantly potamophilous and its range of distribution includes mainly the countries adjoining the Baltic Sea.

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## Marine fish:

<u>Gadus morrhua</u>	Intestine	Baltic Sea (Gulf of Finland)
<u>Rombus maximus</u>	"	"
<u>Zoarces viviparus</u>	"	"
<u>Clupea harengus membras</u>	"	"
<u>Pleuronectes flesus</u>	"	"

## Migratory fish:

<u>Salmo salar</u>	Intestine	Baltic Sea, Elbe, Tay
<u>Salmo trutta</u>	"	Baltic Sea (Gulf of Finland)
<u>Osmerus eperlanus</u>	"	"
<u>Anguilla vulgaris</u>	"	"

## Freshwater fish:

<u>Acanthopterygii:</u>	1	Intestine	) Baltic Sea (Gulf of Finland. Lake Onega (Russia)
<u>Physostomi:</u>	9	"	

All the marine fish mentioned above live in the brackish water regions of the Baltic Sea where they presumably also infected themselves with the acanthocephalan. Even the migratory fish may infect themselves with this parasite in brackish waters. According to SCHNEIDER, Pontoporeia affinis, an amphipod which lives both in fresh and brackish water, acts as intermediate host. It is likely that in the North Sea a similar arthropod form acts as intermediate host and the migratory fish living there, in particular Salmo salar, become infected with Echinorhynchus salmonis in the mouth of the river, in brackish water.

Acanthocephalus lucii (MÜLL.). This parasite is even more strongly potamophilous; at the same time this acanthocephalan is widely distributed among marine and freshwater fish. This is possible particularly on account of its intermediate host, Asellus aquaticus, which is very common and widely distributed itself.

By accidentally swallowing such an arthropod, the Tweed salmon which TOSH (99) had once found infected with Acanthocephalus lucii, could have become infected with that parasite in fresh or brackish water.

Marine fish:

<u>Acanthopterygii:</u>	6	Intestine	) Atlantic Ocean.
<u>Anacanthini:</u>	6	"	) Mediterranean. North and
<u>Physostomi:</u>	2	"	) Baltic Seas

## Migratory fish:

<u>Salmo salar</u>	Intestine	Tweed
<u>Salmo trutta</u>	"	Sweden
<u>Coregonus oxyrhynchus</u>	"	? (according to LÜHE)
<u>Anguilla vulgaris</u>	"	Trieste. Ems. Baltic Sea

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## Freshwater fish:

<u>Acanthopterygii:</u>	5	Intestine	) Northern and Central Europe
<u>Anacanthini:</u>	1	"	
<u>Physostomi:</u>	22	"	

Pomphorhynchus laevis (Zoega). This parasite which is very common in marine and freshwater fish, is found occasionally also in Salmo salar, mostly encapsulated in the peritoneum. Very rarely it is also found in the intestine as a mature worm; only once in a Scottish salmon. In Rhine salmon it has always been found in larval stages. ZSCHOKKE (112) found it 4 times in 129 Rhine salmon; among 170 similar fish I found ~~it~~ only twice ~~in~~ 4 specimens. These larvae agreed completely with the picture described by HAMANN for Pomphorhynchus laevis, and the most advanced acanthocephalan had almost exactly the same appearance as HAMANN depicted for the larva of Phoxinus laevis. Therefore it is not necessary to give any morphological details here.

As KOEHLER (45) has demonstrated, encapsulated Pomphorhynchus laevis often die if they cannot develop further. ZSCHOKKE has shown that the acanthocephalans which encapsulated in the salmon, have the same fate (112). This is the same phenomenon we

have encountered frequently in cestodes (Coenomorphus grossus) and in nematodes (Ascaris capsularia).

Of all acanthocephalans, we probably know most about the mode of life of Pomphorhynchus laevis. I refer here in particular to the studies by HAMANN (33,34), ZSCHOKKE (113) and FEHLMANN (21).

Salmo salar is known as <sup>final</sup> ~~main~~ and as intermediate host, both in the Rhine and in Scottish rivers. It is difficult to say how the fish become infected in either case. A few speculations shall be discussed here; for further details, reference should be made to the biological-faunistic part.

In the Rhine, HERMANN (37) and HOEK (40) found Pomphorhynchus laevis as mature worms in young salmon descending to the sea. Would it not be possible for young salmon to infect themselves with eggs? From those eggs the embryos hatch which attach themselves somewhere in the body cavity, encapsulate themselves, and stay there throughout descent and ascent and the stay of the fish in the sea. 75

Here again certain Gasterosteus species, which are known to act as hosts and intermediate hosts of Pomphorhynchus laevis, might play a part.

Occasionally Pomphorhynchus laevis was observed in marine fish, a fact which is very strange and which ZSCHOKKE (112) therefore

regarded with great suspicion. It would be possible to explain the occurrence of the parasite in marine fish, particularly in predatory coastal fish, by its wide geographical distribution and the large number of possibilities for infection. According to a helpful communication by Professor Dr. ZSCHOKKE, Pomphorhynchus laevis also occurs as a rare guest in dolphins. These voracious predators may easily become infected with the parasite by feeding on migratory fish, in particular on the larva-carrying salmon and the marine trout.

The following list provides information on its hosts and its distribution.

Marine fish:

<u>Acanthopterygii:</u>	8	Intestine	)	Baltic Sea, North Sea.
<u>Anacanthini:</u>	7	"	)	Atlantic Ocean
<u>Physostomi:</u>	2	"	)	(American coast)

Migratory fish:

<u>Salmo salar:</u>	Intestine: also	Tweed, Rhine, White
	encapsulated	Sea?
<u>Salmo trutta</u>	Intestine	? (according to LÜHE)
<u>Osmerus eperlanus</u>	"	? (according to PFEILER)
<u>Alosa vulgaris</u>	"	Memel
<u>Anguilla vulgaris</u>	"	Wurttemberg
<u>Acipenser sturio</u>	"	Baltic Sea, Upper Italy
<u>Acipenser huso</u>	"	?
<u>Acipenser ruthenus</u>	"	?

Freshwater fish:

<u>Acanthopterygii:</u>	5	Intestine	}	Europe
<u>Anacanthini:</u>	1	"		
<u>Physostomi:</u>	39	"		

Mammals:

Dolphins according to ZSCHOKKE

Echinorhynchus truttae SCHRANK. It is still very doubtful whether this parasite belongs to the parasitic fauna of Salmo salar, for the reports on salmon infected with it are rather uncertain. Once, in the Vienna Helminthic Collection, it is reported to have been found in salmon, and HERING (36) mentions it a second time from salmon in his "Parasitic fauna of Wurttemberg". More accurate morphological details and details on the origin of the infected salmon are lacking.

There are also only a few data on its occurrence in other fish:

Marine fish:

<u>Opsanus tau.</u>	Intestine	North America (Atlantic coast)
<u>Salmo erythraeus?</u>	"	Bering Islands

Migratory fish:

<u>Salmo salar</u>	Intestine	Neckar? Vienna?
<u>Salmo trutta</u>	"	Prussia

Freshwater fish:

<u>Thymallus vulgaris</u>	Intestine	Göttingen, Vienna
<u>Salmo fario</u>	"	Prussia

It is also impossible to say from the available information whether the parasite is predominantly marine or potamophilous. Therefore we cannot make any statements on the place and manner of infection of Salmo salar.

MÜHLING (72) includes also Echinorhynchus truttae in his list of parasites of Salmo salar. This seems to have been a mistake

for both in the text of his report and in its many quotations from NEUMANN this acanthocephalan is not once mentioned as having been found in Salmo salar. Thus this parasite should be deleted from the list of parasites of East Prussian salmon.

g. Potamophilous forms:

Neorhynchus rutili (ZED.). ZSCHOKKE (114) found this acanthocephalan once in a Dutch salmon. From the locality it seems that the fish was infected with the purely potamophilous parasite in the mouth of the river, similar to the frogs of Pillau on which MÜHLING reports (72). The following list shows its hosts and its geographical distribution: 77

Migratory fish:

<u>Salmo salar</u>	Intestine	Lower Rhine
<u>Salmo trutta</u>	"	Sweden
<u>Anguilla vulgaris</u>	"	Finland, Lake of Lucerne

Freshwater fish:

<u>Acanthopterygii:</u>	4	Intestine	) Region of Baltic Sea.
<u>Anacanthini:</u>	1	"	) Sweden. Northern Germany.
<u>Physostomi:</u>	24	"	) Switzerland, Turkestan

The occurrence of Neorhynchus rutili in the frogs of Pillau and in the stomach of Emys orbicularis must be regarded as pseudo-parasitism. Its wide distribution and the fact that ~~f~~<sup>are</sup> of all salmon parasites it has the highest northward range ~~is~~<sup>are</sup> of great geographical interest. Neorhynchus rutili is found frequently in the Lake of

Lucerne; in the Lake of Davos (1,560 m above sea level) I found it in Salmo lacustris, and in Turkestan it was found in fish from the Issyk-Kul Lake (1,615 m above sea level).

OLSSON (79) mentioned Leuciscus phoxinus, VILLOT (101) the larva of Sialis (niger) flavilatera as intermediate host. Nephelis octoculata and Limnaea are also reported to be intermediate hosts.

Uncertain acanthocephalan species. In 1777, O.F.MÜLLER reported that he had found Echinorhynchus specimens in salmon. He did not give any details on his find and its locality. It appears from publications by later authors like GOEZE, ZEDER, RUDOLPHI and WESTRUMB that those acanthocephalans from salmon were presumably identical with Pomphorhynchus laevis (ZOEGER).

In 1902, SCHNEIDER (90) examined several fish from the Finnish reef belt for their parasitic fauna. In the intestine of a salmon he found, in addition to specimens of Abothrium crassum, an acanthocephalan larva which according to his findings had entered the salmon by the latter's feeding on a "Strömling" (translator's note: no equivalent was found for this German word; it is a kind of small herring in the Baltic) (Clupea harengus membras). Morphological details are lacking.

In his list of salmon parasites published in 1872, HERING (36) mentions not only Echinorhynchus truttae, but also another

acanthocephalan which he allegedly found in the intestine of a salmon. He identified it as Echinorhynchus Anthuris (DUJ.), but had grave doubts about it himself because the specific name is followed by a question mark and that in turn by the name of the host typical for that parasite (in brackets Triton). According to DUJARDINS (20), that parasitic species is known only from Triton cristatus and Triton punctatus.

In order to avoid possible errors, brief reference shall be made to the following Echinorhynchus species appearing in the literature on salmon parasites:

? nodulosus RUD. 1809/10 (87). WARD (103) put the generic name Echinorhynchus in front of the question mark.

Echinorhynchus nodulosus RUD. nec. WARD is synonymous with Pomphorhynchus laevis (ZOEGA).

Echinorhynchus inflatus RUD. 1809/10 (87) is synonymous with Echinorhynchus salmonis (see in McINTOSH - 64 - 1863).

Echinorhynchus fusiformis RUD. 1819 is synonymous with Echinorhynchus truttae.

Echinorhynchus salmonum RUD. 1819 (88) is the collective name for several questionable Echinorhynchus species which were abolished later because they were synonymous with Pomphorhynchus laevis (ZOEGA). Therefore Echinorhynchus salmonum RUD. is also

synonymous with Pomphorhynchus laevis (ZOEGA).

(e) Parasites from American and Asiatic salmon: Since in the faunistic-biological part frequent reference will be made to parasites from American and Asiatic Salmonidae, I shall give a brief systematic description of those species which have not already been discussed in the previous chapters of the systematic part.

(1) Trematodes:

Unfortunately, reports on the occurrence of trematodes in Pacific Salmonidae are very scarce. According to WARD (103), C. RUTTER examined 200 young salmon in fresh water. In 31 specimens parasites were found which belonged to 2 or 3 species. From the short diagnosis given by RITTER, WARD assumes that they were cestodes and trematodes.

As the material referred to above and the reports on it 79 are very uncertain, I shall not discuss them any further.

Azygia sebago WARD. With regard to its appearance and its systematic classification, this trematode which parasitizes Salmo salar sebago has its parallel in the European species Azygia tereticollis (RUD.). It is purely potamophilous and seems to parasitize various freshwater fish from the North American lakes.

WARD found it in the following hosts:

Migratory fish:

<u>Anguilla chrysopa</u>	Stomach	}
<u>Osmerus mordax.?</u>	Esophagus and stomach	

Freshwater fish:

<u>Salmo salar sebago</u>	Stomach	}	Lake Sebago (North America)
<u>Esox reticulatus</u>	"		
<u>Perca flavescens</u>	"		

According to WARD (103), the trematodes identified as Azygia tereticollis by STAFFAED (95) do not belong to that species, but to Azygia sebago. This would add the following three hosts to the above list for Azygia sebago:

<u>Esox lucius</u>	Gullet, esophagus and stomach	}	Canada (Montreal)
<u>Lota maculosa</u>	" " "		
<u>Ameiurus nigricans</u>	" " "		

(2) Cestodes:

I have already mentioned RUTTER's finds which were published by WARD (103). They were presumably Abothrium crassum (BLOCH).

When describing the life cycle of the Alaska salmon (Oncorhynchus nerca), BEAN, too, reports the occurrence of numerous intestinal parasites, but names and details are lacking.

On the basis of abundant material, ZSCHOKKE and HEITZ (116) report parasites from various salmonid species, among them also cestodes some of which have become known from European salmon, too.

and some of which are not found among those parasites.

Pelichnibothrium caudatum ZSCHOKKE. The larval form of a cestode still unknown in its mature stage and called Pelichnibothrium caudatum by ZSCHOKKE (116) is frequently found in large numbers in the intestine of Oncorhynchus tshawytscha, O.nerca 80 and O.keta. This worm is purely marine. Presumably it develops into the mature worm only in the large predatory fish of the sea. The above-mentioned Oncorhynchus species are therefore only intermediate hosts.

Bothriocephalan larvae. Similar to Salmo salar, which acts as intermediate host for various parasites, carrying their larvae, the Oncorhynchus species, too, seem to carry larvae. Pelichnibothrium has already been mentioned. Apart from that parasite, bothriocephalid larvae were also found in Oncorhynchus nerca which, however, could not be identified.

Sparganum sebago, larva, I,II WARD. These 2 bothriocephalid larvae were found in 2 salmon from Lake Sebago, the smaller form in the spleen, the larger form free in the body cavity. Other intermediate hosts, hosts or developmental stages are unknown. No biological or faunistic details are available.

Proteocephalus pusillus WARD. This cestode, found by WARD (103) in the intestine of Salmo salar sebago, belongs to the large group of parasites of Proteocephalidae which mostly parasitize freshwater fish. In addition to mature individuals, WARD also found two larval forms which can be regarded as developmental stages of Proteocephalus pusillus. A third larva was very similar to the two above-mentioned ones, too, but WARD could not make up his mind to identify it with the others.

WARD's pupil, LA RUE, published a detailed, comprehensive paper in 1914 on all members of Proteocephalidae known until then. He not only mentions Salmo salar sebago as a host of Proteocephalus pusillus, but also Cristivomer namaycush (WALB.), a trout species from Lake Temagani (Ontario). This makes the parasite an exclusive salmonid parasite of purely potamophilous character, a fact which 81 already WARD had stressed in his paper.

In Salmo salar sebago, the parasite lives in the esophagus and the intestine, in Cristivomer namaycush, in the intestine and the pyloric appendages.

### (3) Nematodes:

Nematode A and nematode B WARD. In Salmo salar sebago, WARD (103) and one of his pupils found 2 nematode forms which were called Nematode A and Nematode B. Nematode B, which lives in the

body cavity and systematically belongs to the Filaria, seems to be a marine species, for WARD found it very frequently also in Oncorhynchus nerca. Unfortunately we do not have any morphological details on these nematodes. Nematode A, which was found partly in the stomach, partly in the body cavity, seems to be identical with Nematode B; therefore it presumably <sup>is</sup>/also a marine parasite.

How these two species entered the salmon from Lake Sebago which usually is infected only by potamophilous parasites, I cannot say because I do not know the hydrographic conditions of the lake.

#### (4) Myxosporidia:

Henneguya zschokkei GURL. This parasite was found underneath the skin of Oncorhynchus keta and Oncorhynchus kisutch in East Kamtchatka. Further details on its distribution and occurrence may be found elsewhere (116). It is a typical, purely potamophilous parasite of Salmonidae from various Swiss lakes, lakes of Finland and Western Russia, and recently also from Kamtchatka.

### 3. Ectoparasites

Very rarely have ectoparasites been found on Salmo salar, and observations on them are therefore scarce and incomplete. The number of species is small and of partly marine, partly

potamophilous origin. When changing the medium, the migratory fish lose either one or the other. Earlier authors wanted to use this very fact to explain the migration of salmon: salmon migrated from one medium to the other in order to rid themselves from their torturers, they cleanse themselves of their parasites.

(a) Hirudinea

Piscicola geometra LIN. This ectoparasite is very widely distributed and known as parasite of many freshwater fish. On Rhine salmon it was found by ZSCHOKKE (114) only in 1896, while FRITSCH (24) reports as early as in 1894 that the fish leech as an exception also attacked the Elbe salmon. According to a report in the "Fischereizeitung" 1905 (22), Baltic Sea salmon are also infected by these bloodsuckers, often so severely that they die from their injuries. I never found this parasite.

It lives in the body skin (particularly near the dorsal fin) and in the gills.

Cystobranchus respirans Trosch. This parasite is rarer than the above-mentioned ectoparasite. On Rhine salmon it has been found only twice, once by ZSCHOKKE in 1889 (the find was not published then) and a second time by HOEK (40) in 1899. According to HOEK, this purely potamophilous parasite attacks both old and

young salmon. From the reports of various authors it seems that the range of distribution of Cystobranchus respirans is limited to the Rhine and its tributaries. Finds are reported from the Rhine, the Sieg river, Nagold river (Neckar), and the Sihl river (Switzerland). It may also be mentioned here that according to reports by KESSLER (91) the parasite also lives in Lake Onega.

The parasite lives on the body skin, preferably, however, at the origin of the fins.

(b) Copepods

Lepeophtheirus Strömii BAIRD. McINTOSH (64) found this ectoparasite on the adipose fin, the origin of the caudal fin, at the margin of the eye sockets and on the gills of young salmon 83 descending to the sea. It is an interesting fact that he found more male (4) than female (3) individuals, as usually the opposite is true of parasitic copepods.

Salmo salar and Salmo trutta are the only fish known to be infected with Lepeophtheirus Strömii. The fact that the parasite prefers young salmon may indicate that its character is mainly potamophilous, although the family Caligidae, to which Lepeophtheirus Strömii belongs, is rather marine.

Lernaeopoda salmonea LIN. This parasite, found for

the first time in Salmo salar in 1751, sucks on the gills. It has never been observed on Rhine salmon. FRITSCH (24), however, reports that fishermen found this parasite twice on salmon; unfortunately, we do not know whether on Elbe or Baltic Sea salmon. The latter seems to be more likely because the first find was on a Swedish salmon which surely came from the Baltic Sea; also, WEGENER reports on two individuals found in Königsberg. Therefore the range of distribution of this parasite would be limited to the Baltic Sea. Salmo salvelinus is also mentioned as host of this parasite.

Lernaepoda carpionis KRAEY. This parasite, found on the gills of Salmo salar from Greenland and Iceland, also belongs to the genus Lernaepoda. I have no further details on the locality. This species, similar to the preceding one, is presumably marine.

Argulus coregoni THORELL. This copepod, belonging to the Branchiura, often parasitizes, according to FRITSCH (24), salmon from the Elbe and Moldavia. Of purely potamophilous character, Argulus coregonus frequently attacks in large numbers the salmon ascending from the sea in late summer. FRITSCH, for instance, found once a salmon to which more than 60 specimens of this fish louse were attached.

Argulus coregoni clings to the fins, occasionally also to

the body. In addition to Salmo salar, it also parasitizes whitefish, graylings and trout.

According to BEAN and RUTTER (103), the Oncorhynchus 84  
species in the vast rivers <sup>Flowing</sup> ~~falling~~ into the Pacific Ocean are also infected with parasitic copepods. BEAN reports that Oncorhynchus nerca is often more or less "covered". RUTTER found the gills of Oncorhynchus tshawytscha infected with such parasites. The remark "in fresh water" indicates parasites with potamophilous habitat which attack Oncorhynchus species only in fresh water, similar to Argulus.

For completion's sake, one, and to my knowledge the only serious fish disease to afflict salmon, may be mentioned here.

Frequently, in particular in the years 1877-1882, a fish disease was observed in the English and Scottish rivers which caused serious damage to the salmon in those rivers. It is known as salmon pest and it is caused by Bacillus Salmonis pestis which was discovered by PATTERSON.

For further details on this disease, reference can be made to the publication by HOFER (42) on fish diseases.

### III. Comparative faunistic part

#### 1. Rhine salmon and its parasitic fauna

From the chronicle of research into salmon parasites we see that Rhine salmon has repeatedly been the subject of various biological, physiological and especially parasitological studies. To make this review as complete as possible, I would like to precede the results of my own studies by a list of all parasitological finds made in Rhine salmon in the course of almost 150 years.

- |  |  |
|--|--|
| ca. 1770. HERMANN (37): <i>Echinorhynchus salmonis</i> in einem Sälmling.  | → ..in a young salmon.   |
| 1779. BLOCH (10): <i>Taenia crassa</i> (= <i>Abothrium crassum</i> ).  |  |
| 1781. PALLAS (82) <i>Taenia tetra gonoceph</i> (= <i>Abothrium crassum</i> ).  |  |
| 1782. HERMANN (37): Veröffentlichung seiner um das Jahr 1770 gemachten Funde: <i>Echinorhynchus salmonis</i> (= <i>Pomphorhynchus laevis</i> ).  | Publication of his finds made at approx. 1770                  |
| 1885. PRENANT (84): <i>Filaria piscium</i> (= <i>Ascaris capsularia</i> ) (Mosellachs).  | → Moselle salmon   |
| 1872. HERING (36): <i>Derozenes variicus</i> ; <i>Abothrium crassum</i> ; <i>Ascaris capsularia</i> ; <i>Echinorhynchus truttae</i> ; <i>Echinorhynchus Anduris?</i> (wahrscheinlich aus Neckarlachs gesammelt).   | (presumably collected from Neckar salmon)                      |
| 1889. ZSCHOKKE (110): <i>Derozenes variicus</i> , <i>Distomum reflexum</i> , <i>Distomum Miescheri</i> ; <i>Abothrium crassum</i> , <i>Bothriocephalus spec.</i> , <i>Coenomorphus grossus</i> , <i>Tetrarhynchus paleaceus</i> ; <i>Ascaris capsularia</i> , <i>Ascaris clavata</i> ; <i>Echinorhynchus spec.</i>   |  |
| 1891. ZSCHOKKE (112): <i>Derozenes variicus</i> , <i>Distomum reflexum</i> , <i>Distomum Miescheri</i> ; <i>Schistocephalus gasterostei</i> , <i>Abothrium crassum</i> , <i>Bothriocephalus osmeri</i> , <i>Bothriocephalus spec. I, II (larva)</i> , <i>Tetrarhynchus paleaceus</i> , <i>Coenomorphus grossus</i> , <i>Tetrarhynchus quadrirostris</i> ; <i>Ascaris adunca</i> , <i>Asc. angulata</i> , <i>Asc. clavata</i> , <i>Asc. capsularia</i> , <i>Asc. communis</i> ; <i>Echinorhynchus gadi</i> , <i>Neorhynchus agilis</i> , <i>Pomphorhynchus laevis</i> .<br>Unerwähnt geblieben: <i>Cystobranchnus respirans</i> . |  |
| 1896. ZSCHOKKE (114): <i>Abothrium crassum</i> , <i>Coenomorphus grossus</i> , <i>Bothriocephalenlarven</i> ; <i>Brachyphallus crenatus?</i> ; <i>Ascaris adunca</i> , <i>Asc. spec. I und II</i> , <i>Ascaris capsularia</i> ; <i>Echinorhynchus spec.</i> , <i>Neorhynchus agilis</i> , <i>Neorhynchus rutili</i> ; <i>Piscicola geometra</i> .  | → Remained unmentioned: <u><i>Cystobranchnus respirans</i></u> |
| 1897. HAUSMANN (35): <i>Derozenes variicus</i> , <i>Distomum reflexum</i> , <i>Brachyphallus crenatus</i> (= <i>Distomum appendiculatum</i> (= <i>Dist. ocreatum</i> )).   |  |
| 1899. HOEK (39): <i>Ascaris clavata</i> ; <i>Pomphorhynchus laevis?</i> ; <i>Cystobranchnus respirans</i> (in Holland gesammelt).  |  |

(collected in Holland)

Already these few data show that the Rhine salmon has an unusually rich parasitic fauna.

In order to prevent confusion of the following, I will make a few brief remarks, criticizing and clarifying the above-mentioned finds, in particular those by ZSCHOKKE.

The finds made before 1889 are not taken into consideration in the following discussion and particularly in the statistical summaries. I have also disregarded those by HAUSMANN (35) because they are too restricted (only trematodes). Those by ZSCHOKKE which that author made in Baltic Sea and North Sea salmon, will be specially discussed in the second division of the comparative part.

Therefore only ZSCHOKKE's finds from Rhine salmon in 1889, 1891 and 1896 remain. I would like to make it quite clear that all parasitic species reported by ZSCHOKKE in 1889, are included in his paper published in 1891. In order to avoid errors we must therefore remember that the 45 salmon examined in 1889 are included in the 129 salmon from 1891. 8 specimens from 1896 are to be added to those 129, and thereby we arrive at a total number of 137 of Rhine salmon examined. The infection percentages in Table II refer to these 137 and not to the 129 (as in Table I by ZSCHOKKE, 1891).

Various points in the lists of parasites compiled by ZSCHOKKE have to be clarified. In 1891 he enumerates 33 forms on the basis

of his own and other authors' finds. Of those, however, Bothriocephalus cordiceps LEIDY which was only included by mistake, must be deleted. Also, Leuckartia spec. MONIEZ must be removed from the list as synonymous with Abothrium crassum (BLOCH), Tetrarhynchus solidus DRUM.) as synonymous with Coenomorphus (Tetrarhynchus) grossus (RUD.), Distomum appendiculatum RUD. as synonymous with Distomum ocreatum RUD., and the two latter species as synonymous with Brachyphallus crenatus (RUD.), or, rather, they must be replaced by the correct specific names. Thereby the list of 1891 shrinks to 29 species. In 1896 it is extended to include 37 species by including Scolex pleuronectis MÜLL., Bothriocephalan larvae ZSCHOKKE 1896, Tetrarhynchus spec. ZSCHOKKE 1896, Ascaris spec. I and II ZSCHOKKE 1896, Neorhynchus rutili (MÜLL.), Echinorhynchus spec. ZSCHOKKE 1896 and Piscicola geometra 88 LIN. as new salmon parasites.

The list of parasites for the Rhine salmon is naturally shorter than the list for all salmon. In 1896, it comprises only 26 species (20 species of 1891, excluding Tetrarhynchus solidus DRUM. as synonymous with Coenomorphus (Tetrarhynchus) grossus (RUD.), and including the ectoparasite Cystobranthus respirans TROSCH which had at that time been left unmentioned; also ~~6~~ species of 1896).

In the course of my parasitological studies, I found a large number of parasites already known from salmon, and on and in

Table II.  
TABELLE II.

Parasiten: Parasites	Bewohnte Organe: Organs where they lived	A		B		C
		von 170 infiziert	%	von 137 wdh. viel zu infiz. b. Zschokke	Anzahl von Parasiten:	
1. <i>Derogenes varicus</i> (MÜLL.).	Ösophag, Magen	64	37,64	14,59	455	
2. <i>Brachyphallus crenatus</i> (RUD.).	Ösophag, Magen.	9	5,39	3,64	53	
* 3. <i>Lecithaster gibbosus</i> (RUD.).	Ösophag, Magen, Darm	2	1,17	—	2	
4. <i>Distomum Miescheri</i> ZSCHOKKE.	Ösophag, Magen.	3	1,75	2,19	3	
* 5. <i>Crepidostomum farionis</i> (MÜLL.).	Darm.	1	0,59	—	1	
* 6. <i>Azygia tereticollis</i> (RUD.).	Magen.	1	0,59	—	1	
7. <i>Abothrium crassum</i> (BLOCH).	Appendices pyloricae, Darm.	99	58,23	43,79	252	
8. <i>Tetrarhynchus quadrirostris</i> (GZE.).	an Leber, Peritoneum, Ösophag- und Darmwand; zwischen den Append. pyl.	12	7,05	8,02	16	
* 9. <i>Tetrarhynchus erinaceus</i> v. BEN.	zww. d. Append. pylor.; eingekaps. i.d. Ösophagwand.	2	1,17	—	2	
10. <i>Coenomorphus grossus</i> (RUD.).	zwischen den Append. pylor.; an Leber, Peritoneum	5	2,94	3,64	5	
* 11. <i>Tetrabothrium spec.</i> HEITZ.	im Enddarm.	1	0,59	—	1	
* 12. <i>Scolex pleuronectis</i> MÜLL.	in Append. pylor.	1	0,59	—	1	
13. <i>Ascaris capsularia</i> RUD.	an Leber, Peritoneum, Darmwand, Append. pyl. Ösophag (meist eingekapselt).	140	82,35	72,26	554	
14. <i>Ascaris adunca</i> RUD.	Ösophag, Magen; seltener im Darm.	9	5,39	2,19	116	
15. Unbestimmte Nematoden Unidentifiable nematodes	meist in verkalkten Cysten im Peritoneum und zwischen den Append. pylor.	12	7,05	1,45	13	
16. <i>Pomphorhynchus laevis</i> (ZORGA).	außen an Append. pylor. und Darm.	4	2,35	2,91	5	
* 17. <i>Echinorhynchus heteracanthis</i> HEITZ.	zwischen den Append. pylor.	1	0,59	—	1	

\*Für den Rheinlachs neu.  
New for Rhine salmon

Anzahl der in 170 Rheinlachsen  
gefundenen Parasiten: 1481.  
Number of parasites  
found in 170 Rhine salmon:  
1481

A - how many infected of 170?      B - how many % infected of 137, according to ZSCHOKKE      C - number of parasites

- |   |  |
|---|--|
| 1 - pyloric appendages, intestine   | 7 - on liver, peritoneum, intestinal wall, pyloric appendages, esophagus (mostly encapsulated) |
| 2 - on liver, peritoneum, esophageal and intestinal walls; between pyloric appendages | 8 - esophagus, stomach; more rarely in intestine   |
| 3 - between pyloric appendages; encapsulated in esophageal wall                       | 9 - mostly in calcified cysts in peritoneum and between pyloric appendages                     |
| 4 - between pyloric appendages; on liver, peritoneum                                  | 10 - outside on pyloric appendages and intestine   |
| 5 - in terminal intestine   | 11 - between pyloric appendages  |
| 6 - in pyloric appendages   |  |

the same organs, in approximately the same numbers and frequency as ZSCHOKKE did before. There were only a few species I did not find, but they were parasites which occur in salmon very rarely, some of them had even been found in salmon only once. These forms presumably are purely accidental guests. In their place I found parasites some of which were known from other hosts, but new for salmon, others of which had never been encountered before in salmon or any other animal. Their occurrence in Salmo salar seems accidental, too, for nobody will deny that such purely potamophilous forms as Crepidostomum farionis and Azygia tereticollis do not belong to the parasitic fauna of salmon.

Table II summarizes all parasites I found in Rhine salmon, their occurrence and the organs in which they were found. Table III reviews the number, name, and types of origin of all parasites so far known from salmon.

Of the species listed in Table III, only 8 are found frequently in Rhine salmon, namely Derogenes varicus, Brachyphallus crenatus, Abothrium crassum, Tetrarhynchus paleaceus, Tetrarhynchus quadrirostris, Coenomorphus grossus, Ascaris capsularia, and Ascaris adunca. All others were found rarely, some of them only once.

Of the 8 parasitic species listed as frequent, only 3 can be found always and in greater or smaller numbers both in Rhine

salmon and in salmon from other rivers. We see from Table II that Derogenes varicus, Abothrium crassum and Ascaris capsularia infect a large percentage of Rhine salmon. Ascaris capsularia is most frequent. Less frequently salmon are infected by the typical freshwater and salmonid parasite Abothrium crassum. Rarely more than 10 specimens are found; mostly there are only 2-4. I, at least, have never found as strong an infection as reported by ZSCHOKKE (112) and also SCHNEIDER (90,91). Derogenes varicus, the last of the three parasites mentioned previously, is least frequent with regard to the number of infected salmon, but it by far exceeds the others with regard to the number of specimens found in one salmon. 20 to 30, even more than 50 specimens of this species in one salmon stomach were not uncommon. Several times many more than 100 individuals of this trematode were collected. They were mostly embedded in the esophageal and gastric mucus. Sometimes the esophagus and stomach, in particular the gastric pouch, were veritable foci of trematode infection.

The other parasitic species are very rare in salmon. Distomum Miescheri, Ascaris adunca, Coenomorphus grossus and Tettrahynchus quadrirostris were always found only in small numbers, the first two in the stomach, the last two in the body cavity. Scolex pleuronectis, Tettrahynchus erinaceus, Lecithaster gibbosus, Azygia tereticollis and Crepidostomum farionis were found in Rhine salmon

for the first time. Tetrabothrium spec. and Echinorhynchus heteracanthis, from the terminal intestine and the body cavity, respectively, are completely new parasitic species.

If we look more closely at this varied, numerous parasitic population which infects Rhine salmon to a greater or lesser degree, it is striking how the marine element dominates. Table III summarizes the results obtained in the systematic part in order to confirm the preceding sentence.

The marine character of the parasitic fauna of Rhine salmon is obvious, for of the 35 parasites 13 are purely marine, 6 potamophilous, and 6 marine-potamophilous; 10 species are of slightly uncertain origin (Distomum Miescheri, Bothriocephalus spec. I and II, bothriocephalan larvae 1896, Tettrarhynchus spec., Tetrabothrium spec., Ascaris spec. I and II, Echinorhynchus spec., Echinorhynchus heteracanthis). Perhaps they belong to the marine group, at least Distomum 90 Miescheri, Tettrarhynchus spec., Tetrabothrium spec. and Echinorhynchus heteracanthis, for these are closely related to forms of purely marine character.

The 6 purely potamophilous parasites are Azygia tereticollis, 91 Crepidostomum farionis, Abothrium crassum, Neorhynchus rutili, Pisciola geometra and Cystobranchus respirans. The last two belong to those ectoparasites which attack freshwater fish of various species

Table III. List of Rhine salmon parasites

Parasiten: Parasites	el- gen: A	In ? Meer- fischen B	In ? Wander- fischen C	In ? Süss- wasser- fischen D	To- tal E
1. ○× <i>Derogenes varicus</i> (MÜLL.).		51	6	3	60
2. ○ <i>Distomum reflexum</i> CREPL.		1	1	—	2
3. ○? <i>Distomum Miescheri</i> ZSCHOKKE.	+	—	1	—	1
4. ○ <i>Leithaster gibbosus</i> (RUD.).		22	4	—	26
5. ○ <i>Brachyphallus crenatus</i> (RUD.).		17	4	—	21
6. × <i>Crepidostomum furionis</i> (MÜLL.).		—	3	5	8
7. × <i>Azygia tereticollis</i> (RUD.).		—	2	10	12
8. × <i>Abothrium crassum</i> (BLOCH.).		—	3	20	28
9. ○ <i>Bothriocephalus osmeri</i> v. LINST.		—	2	—	2
10. ○? <i>Bothriocephalus spec. (larva) I.</i> ZSCHOK.	+	—	1	—	1
11. ○? <i>Bothriocephalus spec. (larva) II.</i> ZSCHOK.	+	—	1	—	1
12. ○? <i>Bothriocephalenlarven</i> ZSCHOKKE.	+	—	1	—	1
13. ○? <i>Tetrabothrium spec.</i> HEITZ.	+	—	1	—	1
14. ○× <i>Scolex pleuronectis</i> MÜLL.		üb. 150	5	4	?
15. ○ <i>Cocnomorphus grossus</i> (RUD.).		24?	3	—	27?
16. ○ <i>Tetrarhynchus quadrirostris</i> (GZE.).		11?	1	—	12?
17. ○ <i>Tetrarhynchus paleaceus</i> RUD.		42	1	—	43
18. ○? <i>Tetrarhynchus spec.</i> ZSCHOK.	+	—	1	—	1
19. ○× <i>Ascaris capsularia</i> RUD.		92?	9?	3?	104?
20. ○ <i>Ascaris communis</i> DIES.		15	1	—	16
21. ○ <i>Ascaris adunca</i> RUD.		21	6	—	27
22. ○ <i>Ascaris clavata</i> RUD.		26	2	—	28
23. ○? <i>Ascaris spec. I.</i> ZSCHOKKE.	+	—	1	—	1
24. ○? <i>Ascaris spec. II.</i> ZSCHOKKE.	+	—	1	—	1
25. ○? <i>Nematodes spec.</i> HEITZ.	+	—	1	—	1
26. ○ <i>Ascaris angulata</i> RUD.		4	1	—	5
27. ×○ <i>Pomphorhynchus laevis</i> (ZOEGL.).		17	8	45	70
28. × <i>Neorhynchus rutili</i> (MÜLL.).		—	3	29	32
29. ×○ <i>Echinorhynchus truttae</i> SCHIRANK.		1	2	2	5
30. ○? <i>Echinorhynchus heteracanthis</i> HEITZ.	+	—	1	—	1
31. ○× <i>Echinorhynchus gadi</i> MÜLL.		59	5	6	70
32. ○ <i>Neorhynchus agilis</i> (RUD.).		8	2	—	10
33. ○? <i>Echinorhynchus spec.</i> ZSCHOKKE.	+	—	1	—	1
34. × <i>Piscicola geometra</i> LIN.		—	+?	+?	+?
35. × <i>Cystobranchus respirans</i> TROSCH.		—	+?	+?	+?

A - specific form    B - in ? marine fish    C - in ? migratory fish  
D - in ? freshwater fish    E - total

frequently and often in large numbers. Their occurrence on Salmo salar can therefore be easily explained. Of greater interest is the occurrence of intestinal parasites which usually are found only

in freshwater fish. I have already discussed my opinion on the manner of infection in the systematic part. I would only like to stress once again that 3 of those parasites are accidental guests, and only Abothrium crassum occurs constantly and in larger or smaller numbers. The figures in Table III show, however, that even that parasite is purely potamophilous.

Of the 6 marine-potamophilous parasitic species, some are more marine, some more potamophilous. As can be seen from the above Table, Derogenes varicus, Scolex pleuronectis, Ascaris capsularia and Echinorhynchus gadu belong to the first, Pomphorhynchus laevis and Echinorhynchus truttae to the second group.

Table IV gives a review of the number of parasitic species individual found in  $\frac{1}{2}$  fish of a particular type of Rhine salmon.

Table IV

A Parasitenarten	B Unter- rhein:	C Mittel- rhein:	D Ober- rhein:	E Mosel:	Total:
mit 0 infiziert waren im	0	0	1	0	1
" 1 " " "	0	2	37	1	40
" 2 " " "	3	2	65	4	74
" 3 " " "	7	3	20	12	42
" 4 " " "	5	0	5	0	10
" 5 " " "	1	0	0	0	1
" 6 " " "	1	1	0	0	2

A - parasitic species

B - Lower Rhine

C - Middle Rhine

D - Upper Rhine

E - Moselle

"mit .. infiziert waren im" - with .. infected were in the

The above Table provides interesting information on two points: on the degree of infection in the individual parts of the river, and on the decrease in the number of parasitic species the higher the salmon ascend the river.

The degree of infection is actually very low. In most cases 92 1 to 3 parasitic species are present, usually the species already mentioned above: Derogenes, Abothrium and Ascaris capsularia. They are occasionally accompanied by a few other species, mostly also by a parasite of the body cavity. Comparing the above Table with the corresponding table by ZSCHOKKE (112), we find considerable agreement: for that author, too, 1-3 species in one host are the ordinary.

Let us now compare the respective columns for Lower, Middle, and Upper Rhine and Moselle with each other. The parasitic situation in the Moselle is similar to that prevailing in the Upper Rhine; there are almost always 1-3 species in the same salmon. Salmon from the Middle Rhine, on the other hand, sometimes display a more varied parasitic fauna, and in salmon from the Lower Rhine this is even the rule. There, no salmon carries none or only one parasitic species. 5 fish are infected by 4 species, and 1 fish each by 5 and 6 species. The opposite is true of salmon from the Upper Rhine: no salmon with 5 or 6 species, few with 4 and 1 even infected by no species; most <sup>of</sup> the fish are infected by 1 or 2 species. We see,

therefore, that the higher the Rhine salmon ascends the river, the more the number of species in its parasitic fauna decreases.

Table V provides an answer to the question whether the number of infected fish also decreases.

Table V

A Parasiten:	B Unterrhein: von 17 Lachsen ?	C Mittelrhein (inkl. Mosel): v. 25 Lachsen?	D Oberrhein: von 128 Lachsen?	E Total: von 170 Rheinlachsen?
<i>Ascaris capsularia</i>	12 = 70,5 %	17 = 68,0 %	111 = 86,7 %	140 = 82,3 %
<i>Derogenes varicus</i>	13 = 76,4 %	17 = 68,0 %	34 = 26,6 %	64 = 37,6 %
<i>Abothrium crassum</i>	13 = 76,4 %	16 = 64,0 %	66 = 51,5 %	95 = 55,8 %

- A - parasites
- B - Lower Rhine; of 17 salmon ?
- C - Middle Rhine (including Moselle); of 25 salmon ?
- D - Upper Rhine; of 128 salmon ?
- E - Total; of 170 Rhine salmon ?

This Table lists only the three most common parasitic species. One glance at the figures for Abothrium crassum and Derogenes varicus immediately convinces us that the number of infected fish among ascending salmon decreases noticeably. In the Lower Rhine the rates of infection is the same for both species because they were found in the same number of salmon. This rate then decreases for Derogenes varicus in the course of the upstream journey of the salmon, so that in the Upper Rhine only 26% of the fish are infected by this parasite. The behaviour of Abothrium crassum differs slightly. The rate of infection decreases more slowly, but nevertheless distinctly; in the Upper Rhine, 51% of the salmon are

still infected. Incidentally, the high rate of infection in the Lower Rhine proves that Salmo salar does not become infected with the purely potamophilous Abothrium crassum, in fresh water, but before that, either in the sea or in brackish water. Could Abothrium crassum therefore be synonymous with Abothrium rugosum from among the gadids, after all? (See systematic part under Abothrium crassum).

The conditions for Ascaris capsularia are in striking contrast to those outlined above for the intestinal parasites Derogenes varicus and Abothrium crassum, for the rates of infection for the Upper and Lower Rhine are approximately the same.

On what does this different behaviour of the three species depend? Derogenes varicus lives in the esophagus and in the stomach, that is to say, in those parts of the digestive tract which are in direct connection with the outer world. Therefore this parasite can easily leave its host through the gullet. This seems to be the case, too, for in the salmon from the Upper Rhine most of these trematodes, usually living in the esophagus and the stomach, were found near the gullet, while the stomach which in salmon from the Lower Rhine is always the main locality of the trematodes, was often completely free from this parasite.

The situation is different for Abothrium crassum. This cestode lives mainly in that part of the intestine which is directly

connected with the pylorus. Moreover, it often is firmly attached with its scolex to the pyloric appendages. It is therefore much more difficult for this parasite than for Derogenes varicus to detach itself and leave the intestine. This is the reason why we still find the parasite in salmon from the Upper Rhine, even if only in small numbers, partly in the pyloric part of the intestine, partly on its way out, in the terminal intestine near the anal opening, and covered with mucus.

Ascaris capsularia, finally, belongs to the parasites of the body cavity. It is thus completely secluded from the outside world and unable to leave the migrating host when it changes its medium or passes through its starvation period. Therefore the rates of infection remain approximately the same, as becomes obvious from Table V.

From the above we see that ascending salmon gradually lose their intestinal parasites. The number of their species decreases, 94 but also the number of specimens of the respective species in an infected salmon, and the number of infected fish.

The numbers of species and of individuals of body cavity parasites, on the other hand, remain constant.

Let us now have a brief look at the seasonal occurrence of parasites in Rhine salmon. The following table will provide

information on the distribution, again of the most common parasitic species, in the individuals months. January and March were disregarded because no fish could be examined during those months, also February, in the course of which only one salmon from the Lower Rhine was examined which, however, had in addition to Coenomorphus grossus, Derogenes varicus and Ascaris capsularia a number of <sup>large</sup> ~~vast~~ specimens of Abothrium crassum.

Table VI

Monate:	Untersuchte Rheinlachs:	Derog. var.	Abothr. crass.	Asc. capsul.
April	4	100,0 %	75,0 %	75,0 %
May	4	100,0 %	50,0 %	75,0 %
June	11	54,5 %	90,9 %	63,6 %
July	3	33,3 %	66,6 %	66,6 %
August	3	66,6 %	—	100,0 %
September	2	—	100,0 %	100,0 %
Oktober	16	43,7 %	43,7 %	75,0 %
November	108	36,7 %	58,3 %	33,3 %
December	18	11,1 %	61,1 %	33,3 %

1 - months

2 - Number of Rhine salmon examined

In spring, Salmo salar, with a large number of parasites, starts its journey upstream. It continues its journey until autumn, reaching its destination in late autumn or early winter and spawning there. In spring and summer, between April and August, the percentage of infected salmon is very high. Towards autumn it decreases and in winter it is at its lowest. ZSCHOKKE made similar observations, and also HAUSMANN gets similar results although he examined salmon for trematodes only in June, July, August and February.

It is immediately obvious that this Table agrees with the preceding one. Here again we notice a distinct decrease of the number of specimens. This decrease differs for the 3 species. It is almost zero for Ascaris capsularia, a parasite of the body cavity, distinctly noticeable for Abothrium crassum, and very great for Derogenes varicus. 95

Let us now briefly consider the behaviour of the other parasites. Of course only those decrease or increase which live in the digestive tract. The parasites of the body cavity and those encapsulated in various organs remain where they are; they cannot move and, as we have seen in the systematic part, most of them degenerate and die. Only <sup>a</sup> few will be able to develop further. "Their numbers can", as ZSCHOKKE (112) has already stressed, "certainly not be increased in the river, only decreased - through the death of individual specimens".

In addition to Derogenes varicus and Abothrium crassum, nematodes, trematodes and occasionally also acanthocephalans and cestode larvae are found in the digestive tract. Some of them leave their hosts on the same way as Derogenes varicus, others pass through the entire intestine and out into the water through the anal opening. Among the first group are Distomum Miescheri and Brachyphallus crenatus, as I could see for myself. Distomum reflexum and Azygia tereticollis, and those specimens of Lecithaster gibbosus

which had not yet passed the pylorus at the onset of the starvation period, go the same way. All parasitic forms living on the other side of the pylorus, go the opposite way. In addition to Abothrium crassum, cestode larvae, Lecithaster gibbosus and Crepidostomum farionis were found in the terminal intestine. Nematodes which have already passed the pylorus go the same way. I found for instance Ascaris adunca in the small intestine and terminal intestine. It is obvious that the parasites leave their hosts, following either way, with the pylorus the dividing line. In salmon descending to the sea after spawning, we find the entire digestive tract almost empty, which HOEK observed also on salmon in Holland after spawning. 96 The last-mentioned author emphasizes in particular the complete absence of Abothrium crassum which inhabits the ascending salmon in such large numbers. Its locality, the pyloric appendages, was completely empty.

From the above it becomes clear that on <sup>their</sup> ~~its~~ journey upstream, salmon gradually lose all their intestinal parasites acquired in the sea; the decrease is proportional to the <sup>duration</sup> ~~length~~ of the journey and the distance travelled. 79

Let us have a look also at the parasites from the viewpoint of their developmental stages in which they are found in Rhine salmon. It is remarkable how many adolescent stages and how few

mature stages are found. If we go through the list of parasites one by one, we find of the 33 endoparasites only 15 either completely mature (Derogenes varicus, Distomum reflexum, Crepidostomum farionis, Azygia tereticollis, Lecithaster gibbosus, Brachyphallus crenatus; Abothrium crassum; Ascaris angulata, Ascaris clavata, Ascaris adunca; Echinorhynchus truttae, Echinorhynchus gadi, Neorhynchus agilis, Neorhynchus rutili) or almost mature (Distomum Miescheri). 18 species are larval stages, among them the cestodes with 10, the nematodes with 5 and the acanthocephalans with 3 forms. Mostly these parasites are encapsulated in or on the intestinal wall, in the liver, in or on the esophageal wall, between the pyloric appendages, etc. Some live freely in the body cavity, e.g. Tetrarhynchus quadrirostris, Coenomorphus grossus, Bothriocephala larvae and Echinorhynchus heteracanthis. Only of two species, namely Tetrabothrium nov.spec. (HEITZ) and Scolex pleuronectis, have larval stages been known to occur together with mature forms, both free in the intestinal lumen. These species, however, as has been mentioned before, are purely accidental guests and would have left their host soon, judging from their locality, like the other mature intestinal parasites.

Below, I would like to review the parasites of Rhine salmon on the basis of the organs they live in.

## I. Digestive tract:

## 1. Esophagus (9 species):

- (a) Specific: Derogenes varicus, Brachyphallus crenatus, Distomum Miescheri, Dist. reflexum.  
 (b) Foreign: Lecithaster gibbosus, Ascaris angulata, Ascaris adunca, Echinorhynchus gadi, Neorhynchus agilis. 97

## 2. Stomach (10 species):

- (a) Specific: Derogenes varicus, Brachyphallus crenatus, Distomum Miescheri, Azygia tereticollis.  
 (b) Foreign: Lecithaster gibbosus, Ascaris adunca, Ascaris spec. I and II, Echinorhynchus gadi, Neorhynchus rutili.

## 3. Intestine (region of pyloric appendages) (3 species):

- (a) Specific: Abothrium crassum, Scolex pleuronectis, Ascaris adunca.  
 (b) Foreign: -

## 4. Intestine (small and terminal intestine) (5 species):

- (a) Specific: Lecithaster gibbosus, Crepidostomum farionis; Abothrium crassum, Tetrabothrium spec., Ascaris adunca.  
 (b) Foreign: 7

## II. Body cavity:

## 1. Peritoneum (7 species):

Coenomorphus grossus, Tetrarhynchus quadrirostris, Tetrarhynchus paleaceus, Ascaris spec., Ascaris clavata, Ascaris capsularia, Pomphorhynchus laevis.

## 2. In the intestinal wall (8 species):

Bothriocephalus osmeri, Bothriocephalus spec. I and II, Tetrarhynchus erinaceus, Tetrarhynchus paleaceus, Tetrarhynchus quadrirostris, Tetrarhynchus spec., Ascaris capsularia.

## 3. On the intestinal wall (11 species):

Bothriocephalus osmeri, Bothriocephalus spec. I and II, Tetrarhynchus quadrirostris, Tetrarhynchus paleaceus, Coenomorphus grossus, Ascaris capsularia, Ascaris clavata, Ascaris spec., Pomphorhynchus laevis, Echinorhynchus heteracanthis.

## 4. Liver (5 species):

Coenomorphus grossus, Tetrarhynchus quadrirostris, Tetrarhynchus paleaceus, Ascaris capsularia, Ascaris communis.

5. Spleen (1 species):  
Ascaris capsularia
6. Kidneys (1 species):  
Ascaris capsularia
7. Genital organs (2 species):  
Tetrarhynchus quadrirostris, Ascaris capsularia.
8. Free in the body cavity (3 species):  
Coenomorphus grossus, Tetrarhynchus quadrirostris, Tetrarhynchus paleaceus.

### III. Ectoparasites:

1. Gills (1 species):  
Pisciola geometra
2. Skin (2 species):  
Pisciola geometra, Cystobranchus respirans.

From this summary we see that most of the parasites live in the body cavity. Since these species, as already mentioned, lie in a separate organ, they are a constant phenomenon for the salmon and are useless for our purposes. Of greater interest are the parasites which live in the digestive tract. 98

With 10 species the stomach is the most populated part of the digestive tract. Infection in the esophagus is equally high. The intestine after the pylorus, on the other hand, has only a few species, the terminal intestine even fewer.

Very many parasites have been found in Rhine salmon in organs where they are usually never found, either in salmon or in

other fish. Ascaris adunca, Ascaris angulata, Echinorhynchus gadi, Neorhynchus agilis and Neorhynchus rutili were found in Rhine salmon in the esophagus and the stomach; all of them lived only in the intestine in other hosts. The two ascarids Ascaris spec. I and II presumably belong to the intestinal fauna, too, because gastric nematodes are rare in fish.

In the intestine itself we do not find any unusual parasites. What, then, is the reason for the parasites in salmon living in other organs than they usually do? ZSCHOKKE interpreted it as a way of seeking protection. To me it rather appears that the above-mentioned parasites are about to leave their host through the gullet. The fact that many intestinal parasites return to the gullet with the gastric and esophageal parasites instead of passing through the entire intestine in the usual way and leave their host through the anal opening, seems to be connected with the onset of the starvation period. Those parasites which at that time have already passed the pylorus, leave the host through the anal opening, the others which are still in front of the pylorus, leave the host through the gullet.

In concluding it may be pointed out that most of the intestinal, mature parasitic species are trematodes. There are only very few cestode and nematode species, and only isolated instances of acanthocephalans, so that in this respect ZSCHOKKE's sentence (108) "les Salmonides ne possèdent pour ainsi dire pas d'Acanthocephales"

seems to apply again. Also with regard to the number of specimens in the fish, the trematodes surpass the cestodes, nematodes and acanthocephalans by far.

Table VII

99

I. Baltic Sea I. Ostsee:		III. Elbe:	
(17 Parasitenarten).		(13 Parasitenarten)	
<b>17 parasitic species</b>		<b>13 parasitic species</b>	
⊗× <i>Derogenes varicus</i> (MÜLL.).	1	⊗× <i>Derogenes varicus</i> (MÜLL.).	1
⊙ <i>Brachyphallus crenatus</i> (RUD.).	2	⊙ <i>Brachyphallus crenatus</i> (RUD.)	4
× <i>Abothrium crassum</i> (BLOCH).	1	⊙ <i>Distomum Miescheri</i> ZSCHOK.	4
×⊙ <i>Schistocephalus gasterostei</i> (FABR.).	4	× <i>Abothrium crassum</i> (BLOCH).	1
×⊙ <i>Triacnophorus nodulosus</i> (PALL.).	4	⊗× <i>Scolex pleuronectis</i> MÜLL.	3
⊙ <i>Bothriocephalus spec. II.</i> ZSCHOKKE.	3	⊙ <i>Coenomorphus grossus</i> (RUD.).	4
⊙ <i>Bothriocephalus spec. III.</i> ZSCHOKKE.	4	⊙ <i>Tetrarhynchus quadrirostris</i> (GZE.).	2
×⊙ <i>Cucullanus elegans</i> ZED.	4	⊗× <i>Ascaris capsularia</i> RUD.	1
⊗× <i>Ascaris capsularia</i> RUD.	2	⊙ <i>Ascaris clavata</i> RUD.	4
⊙ <i>Ascaris adunca</i> RUD.	3	×⊙ <i>Echinorhynchus salmonis</i> MÜLL.	4
⊙ <i>Ascaris communis</i> DIES.	3	⊙ <i>Lernaeopoda salmonca</i> LIN.	3
×? <i>Ascaris aculeati</i> v. LINST.	4	× <i>Argulus coregoni</i> THORELL.	3
×⊙ <i>Pomphorhynchus laevis</i> (ZOEG.)	4	× <i>Piscicola geometra</i> (LIN.).	4
×⊙ <i>Echinorhynchus salmonis</i> MÜLL.	3		
×⊙ <i>Echinorhynchus truttae</i> SCHRANK.	4	IV. Tay:	
⊗× <i>Echinorhynchus gadi</i> MÜLL.	3	(12 Parasitenarten)	
⊙ <i>Lernaeopoda salmonca</i> LIN.	3	<b>12 parasitic species</b>	
		⊗× <i>Derogenes varicus</i> (MÜLL.).	1
II. Tweed:		× <i>Azygia tereticollis</i> (RUD.).	4
(15 Parasitenarten)		⊙ <i>Distomum spec. Mc. INTOSH.</i>	4
<b>15 parasitic species</b>		× <i>Abothrium crassum</i> (BLOCH).	1
⊗× <i>Derogenes varicus</i> (MÜLL.).	1	⊙ <i>Tetrarhynchus quadrirostris</i> (GZE.).	4
⊙ <i>Brachyphallus crenatus</i> (RUD.).	2	⊙ <i>Tetrarhynchus spec. Mc. INT.</i>	4
⊙ <i>Distomum Miescheri</i> ZSCHOK.	4	⊙ <i>Tetralobium minimum</i> v. LINST.	2
× <i>Abothrium crassum</i> (BLOCH).	1	⊗× <i>Ascaris capsularia</i> RUD.	1
⊙ <i>Coenomorphus grossus</i> (RUD.).	3	⊙ <i>Ascaris spec. Mc. INT.</i>	4
⊙ <i>Tetrarhynchus quadrirostris</i> (GZE.).	2	×⊙ <i>Pomphorhynchus laevis</i> (ZOEGA).	4
⊙ <i>Tetralobium minimum</i> v. LINST.	4	×⊙ <i>Echinorhynchus salmonis</i> MÜLLER.	4
⊙ <i>Tetralobium spec. TOSH.</i>	4	×⊙ <i>Lepocithcirus Strömii</i> BAIRD.	4
⊙ <i>Taenia spec. TOSH.</i>	4	<b>V. Pacific Ocean</b>	
⊗× <i>Ascaris capsularia</i> RUD.	1	V. Pacifischer Ozean:	
⊙ <i>Ascaris acuta</i> RUD.	1	(11 Parasitenarten)	
× <i>Ascaris obtusocaudata</i> RUD.	4	<b>11 parasitic species</b>	
×⊙ <i>Pomphorhynchus laevis</i> (ZOEGA).	3	× <i>Abothrium crassum</i> (BLOCH).	2
×⊙ <i>Acanthocephalus lucii</i> (MÜLL.).	4	⊙ <i>Pelichnibothrium caudatum</i> ZSCHOKKE.	1
⊗× <i>Echinorhynchus gadi</i> MÜLL.	4	⊙ <i>Bothriocephalenlarven</i> ZSCHOK. und HERTZ.	4
		⊙ <i>Tetrarhynchus quadrirostris</i> (GZE.).	3

<p>⊙ <i>Coenomorplus grossus</i> (RUD.). 4          ⊙X <i>Ascaris capsularia</i> RUD. 2          ⊙ <i>Filaria</i> WARD. ?          ⊙X <i>Echinorhynchus gadi</i> MÜLL. 2          ⊙ <i>Echinorhynchus caenoformis</i> HERTZ. 4          X <i>Henneguya Zschokkei</i> GURL. 4          X <i>Copepoden</i> WARD. 2</p> <p>VI. Weser:          (10 Parasitenarten)  <b>10 parasitic species</b>          ⊙X <i>Derogenes variatus</i> (MÜLL.). 2          ⊙ <i>Brachyphallus crenatus</i> (RUD.). 4          X <i>Abothrium crassum</i> (BLOCH). 1          ⊙ <i>Tetrarhynchus quadrirostris</i> (GZE.). 3          ⊙X <i>Tetrarhynchus erinaceus</i> v. BEN. 4          ⊙ <i>Coenomorplus grossus</i> (RUD.). 4          ⊙ <i>Tetrobothrium minimum</i> v. LINST. 4          ⊙X <i>Ascaris capsularia</i> RUD. 1          X <i>Ascaris aculeati</i> v. LINST. 4          ⊙ <i>Ascaris adunca</i> RUD. 4</p> <p>VII. North Sea          VII. Nordsee:          (8 Parasitenarten)  <b>8 parasitic species</b>          ⊙X <i>Derogenes variatus</i> (MÜLL.) 3          ⊙ <i>Brachyphallus crenatus</i> (RUD.). 1          X <i>Abothrium crassum</i> (BLOCH). 1          ⊙X <i>Scolax pleuronectis</i> MÜLL. 4          ⊙ <i>Bothriocephalobarsen</i> ZSCHOKK. 3          ⊙ <i>Tetrarhynchus spec.</i> ZSCHOKK. 4          ⊙ <i>Necorhynchus agilis</i> (RUD.). 3          ⊙ <i>Echinorhynchus spec.</i> ZSCHOKK. 4</p>	<p>VIII. Lake Sebago          VIII. Sebago-See:          (7 Parasitenarten)  <b>7 parasitic species</b>          X <i>Azygia sebago</i> WARD. 1          X <i>Abothrium crassum</i> (BLOCH). 1          X <i>Proteocephalus pusillus</i> WARD. 3          X <i>Proteocephalus spec.</i> WARD. 4          X <i>Cestodentaria</i> WARD. 4          X <i>Sparganium spec. I u. II</i> WARD. 4          X⊙? <i>Nematodes A u. B</i> WARD. 3</p> <p>IX. Ireland          IX. Irland:          (5 Parasitenarten)  <b>5 parasitic species</b>          ⊙X <i>Derogenes variatus</i> (MÜLL.). 1          X <i>Abothrium crassum</i> (BLOCH). 1          ⊙ <i>Coenomorplus grossus</i> (RUD.). 3          ⊙X <i>Ascaris capsularia</i> RUD. 1          ⊙ <i>Ascaris clavata</i> RUD. 3</p> <p>X. Canada          X. Kanada:          (4 Parasitenarten)  <b>4 parasitic species</b>          ⊙X <i>Derogenes variatus</i> (MÜLL.). 1          ⊙? <i>Hemirurus appendiculatus</i> (RUD.). 2          ⊙ <i>Iecithaster bothryophorus</i> (OLSS.). 4          ⊙ <i>Sinistrophorus simplex</i> (RUD.). 4</p>
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⊙ = purely marine  
 ⊙X = marine-potamophilous  
 X⊙ = potamophilous-marine  
 X = purely potamophilous

1 = common  
 2 = frequent  
 3 = occasionally  
 4 = rare

## 2. The parasitic fauna of other salmon and salmon species

Not only in the Rhine, but also in many other rivers and in the sea, salmon have been examined for parasites. In the following I would like to compare the results for the Rhine salmon with the results of those other studies, mainly to find an answer to the question whether there are really different types of salmon, ~~was~~ many 101 authors assume, which differ in their nutritional habits depending on the river or sea they live in. The very question whether and why some of them take in food in fresh water, others do not, is as yet unanswered. Perhaps it is possible to solve this question by parasitological methods.

The following salmon are to be compared parasitologically with the Rhine salmon:

Salmon from Canada	Salmon from the Elbe
Salmon from the North Sea	Salmon from the Loire
Salmon from Ireland	Salmon from the Baltic Sea
Salmon from Norway	Salmon from the Tay
The salmon species of the Pacific Ocean	Salmon from the Tweed
Salmon from the Weser	Salmon from Lake Segabo

This comparison may be preceded, for purposes of general orientation, by a list of parasites of all salmon (excluding salmon from the Loire and Norway) (Table VII). The sequence depends on the quantitative magnitude of the parasitic faunas of the

individual salmon.

Table VII reviews the parasitic species, their frequency and their geographical distribution. In order to emphasize the last-mentioned point even more, the most frequent and most widely distributed species have been summarized (including parasites of Rhine salmon; see Table II) as follows:

	of 11 localities in ?	Rate of infection
1. <u>Abothrium crassum</u>	10	1
2. <u>Derogenes varicus</u>	9	1 - 2
3. <u>Ascaris capsularia</u>	8	1 - 2
4. <u>Brachyphallus crenatus</u>	6	2
5. <u>Tetrarhynchus quadrirostris</u>	6	3
6. <u>Coenomorphus grossus</u>	6	3 - 4
7. <u>Echinorhynchus gadi</u>	4	3 - 4

All other species either occur only in 3 or 2 localities or belong only to one river or sea. Locally, they may be quite common and infect salmon to a considerable extent.

It is interesting to note the localities in which the Abothrium crassum occurs everywhere except in Canada, but this cestode is certain to be present even there, as WARD's finds in salmon from Lake Sebago indicate clearly. STAFFORD who examined the Canadian salmon parasitologically, unfortunately published only his findings on trematodes. Derogenes varicus, this gastric parasite which always occurs in large numbers in salmon, can of course not be found in salmon from Lake Sebago, being a

purely marine form; strangely enough, it is also absent from salmon of the Pacific Ocean. In this case, however, insufficient research may be held responsible for its absence. RUTTER found parasites in the stomach of salmon one form of which was interpreted as a trematode by WARD; species and origin are unfortunately unknown. Ascaris capsularia has been found to be absent only in 3 localities, namely in the North Sea, in Canada and in Lake Sebago. For the first locality, this absence can be explained by a scarcity of suitable material, for surely this nematode larva parasitizes also the North Sea salmon, appearing in <sup>all</sup> the parasitic faunas of the salmon ascending from the North Sea. Its absence in Canada will presumably have the same reason as in the case of Abothrium crassum. LINTON mentioned encapsulated nematodes from Salmo salar which from their description and pictures are identical with Ascaris capsularia. Therefore, this species is hardly likely to be missing altogether in the salmon of the Canadian coast.

The other parasitic species are found in considerably fewer localities and, as we can see from the figures, the rate of infection is moderate to low. It is lowest in those which have the smallest range of distribution. Distribution and rate of infection are therefore closely linked with each other.

In addition to Table VII, I would like to use another Table as proof for my further reflections. In this latter Table,

all localities are listed, their parasitic faunas arranged on the basis of their origin (purely marine + marine-potamophilous, potamophilous-marine + purely potamophilous), and the proportions expressed in percentages. To simplify matters, I have listed all parasites known from Oncorhynchus keta, O.nerca and O.tschawytscha under one locality. I also have disregarded all ectoparasites (including Henneguya Zschokkei) and all specific forms<sup>1</sup>, whether 103 their origin is known (Tetrabothrium minimum, Echinorhynchus heteracanthis, Distomum Miescheri) or unknown (Bothriocephalus spec., Ascaris spec., Echinorhynchus spec., etc.). Only those species are to be evaluated which are generally known and of which several hosts are known.

In this manner we have obtained an almost clear picture of the parasitic faunas of salmon from various rivers and seas, so that we can compare the individual habitats and salmon.

Let us now try to establish on the basis of Tables VII and VIII, from the parasitological point of view, the nutritional habits of the individual salmon in the various localities.

The parasitic fauna of Canadian salmon, examined by STAFFORD (95), is unfortunately too incomplete as only trematodes are listed.

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<sup>1</sup> I have used the term "specific forms" for parasitic species which so far have been found only in one fish species and the origin of which - marine or potamophilous - cannot easily be established from migratory fish.

Table VIII

Locality	○	×	Total:	A rein marin	B rein pota- mophil
1. Kanada.	4 = 100,0 %	—	4	3	—
2. Nordsee.	4 = 80,0 %	1 = 20,0 %	5	3	1
3. Irland.	4 = 80,0 %	1 = 20,0 %	5	2	1
4. Pacific.	4 = 80,0 %	1 = 20,0 %	5	2	1
5. Elbe.	7 = 77,8 %	2 = 22,2 %	9	5	1
6. Weser.	7 = 77,8 %	2 = 22,2 %	9	4	2
7. Rhoin.	15 = 71,4 %	6 = 28,6 %	21	11	4
8. Tweed.	7 = 63,6 %	4 = 36,4 %	11	4	2
9. Tay.	3 = 42,9 %	4 = 57,1 %	7	1	2
10. Ostsee.	6 = 42,9 %	8 = 57,1 %	14	3	2
11. Sebagosee.	—	3 = 100,0 %	3	—	3

A - purely marine

B - purely potamophilous

1 - Canada

6 - Weser

2 - North Sea

7 - Rhine

3 - Ireland

8 - Tweed

4 - Pacific Ocean

9 - Tay

5 - Elbe

10 - Baltic Sea

11 - Lake Sebago

It should not surprise us to see that in character and composition the parasitic faunas of salmon from the North Sea and from Ireland agree more or less. Since only marine salmon were examined, only marine parasites were found, with the exception of Abothrium crassum which is a purely potamophilous species (see 104 Tables III and XIV and the systematic part). Coenomorphus grossus and Ascaris capsularia presumably parasitize not only salmon from Ireland, but also from the North Sea, for Rhine, Weser, Elbe and Tweed salmon often carry these forms from the sea into the rivers. Derogenes varicus appears in both types of salmon.

Conditions are similar in Norwegian salmon. I had the opportunity to examine 4 specimens from the coastal regions of Norway for parasites. Their parasitic fauna with Derogenes varicus and Brachyphallus crenatus in esophagus and stomach, with Ascaris adunca in stomach and intestine (with many food remains) and Abothrium crassum in the pyloric region of the intestine can be called almost purely marine. Ascaris capsularia was also found frequently. Therefore Norwegian salmon is parasitologically the same as North Sea salmon.

There is a great difference, on the other hand, between North Sea and Baltic Sea salmon ( to simplify matters, all salmon from the Baltic Sea region examined by different authors have been included; ZSCHOKKE's results, however, are the foundation, for they are the most accurate ones).

Examining the extensive parasitic fauna of the Baltic Sea salmon, we notice immediately the large percentage of potamophilous-marine and purely potamophilous parasites, contrary to the North Sea salmon which has not a single purely potamophilous form (Abothrium crassum always excluded). The only purely potamophilous parasite in the Baltic Sea salmon, with the exception of Abothrium crassum, which according to ZSCHOKKE and SCHNEIDER often occurs in vast numbers, is Ascaris aculeati, but this nematode was always found encapsulated. The only purely marine forms, apart from the ectoparasite

Lernaeopoda salmonea, are Bothriocephala larvae, Ascaris adunca and Ascaris communis. Rhynchobothria larvae, so common in Rhine salmon, are completely missing. ZSCHOKKE explains this different behaviour by the absence of hosts necessary for further development and distribution. All other parasites are either marine-potamophilous or potamophilous-marine.

ZSCHOKKE (112) has the following comment on this phenomenon: "One is automatically tempted to explain this strange behaviour by saying that Baltic Sea salmon take in food even in the river (which, according to NORDQUIST, is allegedly the case) and therefore 105 return to the sea with a parasitic fauna which is much richer in potamophilous forms."

Baltic Sea salmon admittedly can become infected in fresh water with potamophilous forms (Ascaris aculeati, Triaenophorus nodulosus and Cucullanus elegans [questionable: see systematic part]); Rhine salmon do the same. But I think that this happens quite accidentally, as with Rhine salmon. In my opinion this problem is explained by the nature of the Baltic Sea itself.

It is known that large parts of the Baltic Sea, especially in the east, contain fresh water, and the salt content decreases eastward (North Sea 3.44%, Baltic Sea 1.77%, of the latter: Great Belt 1.9%, East Prussian coast 1.2%, Gulf of Bothnia 0.26%). Of

course this has a considerable influence on the fauna and flora of the Baltic Sea. In the Gulf of Finland and the Gulf of Bothnia, particularly in the reefbelt, a vivid exchange takes place between marine and freshwater animals. In these brackish waters both marine and freshwater fish thrive, and marine and potamophilous, low and very low organisms live.

In my opinion, this low salt content of the Baltic Sea and the resultant intermingling of forms are the reasons for the predominantly potamophilous character of the parasitic fauna of Baltic Sea salmon.

It has already been pointed out that the hosts and carriers of mature Rhynchobothria, larger shark species, are missing, and that therefore Baltic Sea salmon is not infected by the larvae of that parasite. Many other, purely marine parasitic species which are common in the North Sea, are frequently or altogether missing. They are replaced by similar species which, however, have completely adapted themselves to their surroundings and infect not only marine, but also potamophilous hosts (Echinorhynchus gadi).

On the other hand, we find many parasites in the Baltic Sea which elsewhere are totally or almost potamophilous. They have become inhabitants of the Baltic Sea, and we find them infecting migratory and purely marine fish (Schistocephalus gasterostei, Triacnophorus nodulosus, Echinorhynchus salmonis, Echinorhynchus

truttae, Pomphorhynchus laevis).

We can make such observations not only in salmon, but also 106 in the other migratory fish of the Baltic Sea like houting and smelt. All of them are more or less infected by such parasites.

Baltic Sea salmon has therefore ample opportunity to become infected with potamophilous parasites even in the Baltic Sea itself. There is also the fact that the Baltic Sea salmon does not change abruptly from one medium to another. The transition is gradual - from sea through brackish water to fresh water. Perhaps the Baltic Sea salmon has become adapted in its life cycle and nutritional habits to this gradual change. It starts its starvation period later during its ascent; perhaps its digestive organs do not degenerate quite as much during the spawning season as in other fish, and it is able during its descent at an earlier time to start taking in food again.

There are unfortunately as yet no detailed systematic studies available on the life and nutrition and the parasitic fauna of Baltic Sea salmon in the rivers. No definite conclusions can be drawn from the isolated, occasional finds in literature.

From what we know about the parasitic fauna and its composition, I would like to draw the cautious conclusion that Baltic Sea salmon undergoes a starvation period in the river similar

in type and duration to that of Rhine salmon. If it really took in food in the rivers, its parasitic fauna would have to be similar to that of Osmerus eperlanus and Coregonus oxyrhynchus (see Tables IX and X).

Conditions are completely different, on the other hand, for salmon living in the North Sea and the adjoining seas and ascending the rivers for spawning which fall into those seas. The parasitic fauna and the habits of spawning salmon have been studied in as many as 6 of those rivers. Two of them belong to the mightiest rivers in Europe, since their springs are situated far inland. We can get the most informative details from those rivers, for in them salmon <sup>have</sup> ~~has~~ to migrate farthest in order to reach the spring streams as its <sup>J.P.</sup> instinct drives it to do. It must, therefore, travel long distances, 107 is exposed to unfavourable influences more than any other salmon, and gives us thereby the best opportunity to study, much better opportunities than salmon ascending only short coastal rivers.

The big rivers in which salmon were examined parasitologically are the Rhine (1,300 km), the Loire (1,000 km), the Weser (with the Werra approximately 700 km), and above all the Elbe (1,150 km). The two smaller rivers are the Tweed (approximately 150 km) and the Tay (approximately 120 km) in Scotland). All these rivers, except the Loire, <sup>flow</sup> fall into the North Sea. Therefore their salmon come from <sup>3?</sup> there.

5 Loire salmon, 1 from the lower and 4 from the upper course of the river, were examined. This material is scarce and we must not consider the results of the examinations as generally applicable. The findings are nevertheless worth mentioning because in spite of the small number of parasites they can be compared with finds from the Rhine (including the Moselle), Weser and Elbe, with interesting results. Ascaris capsularia and Derogenes varicus were never missing, and were always found in the appropriate organs. Large specimens of Abothrium crassum were found in salmon from the lower Loire. Small remains of this cestode were found in 3 specimens from the upper Loire; in one specimen it was entirely missing. Conditions with regard to the trematode fauna were similar. In the lower course of the Loire, salmon were infected by many more than 100 specimens of Derogenes varicus each; in the upper course, however, one salmon had only 20, another one only 9, and the other two even fewer specimens of that parasite each.

From these few specimens, the Loire salmon has therefore the same parasitic fauna as the Rhine and Moselle salmon: only marine parasites, no food in the intestine, and therefore no increase in the parasitic fauna in fresh water. This shows that the salmon presumably does fast on its journey, at least while ascending the streams.

In the Weser salmon I found a greater variety of species than

then in the Loire salmon. I examined 21 Weser salmon. Derogenes vari-  
cus, Abothrium crassum and Ascaris capsularia were again the main  
parasites, being found in 9, 13, and 19 salmon, respectively.  
Other parasites were found, too. Ascaris adunca was encountered in  
a few specimens in stomach and intestine, and Ascaris aculeati  
was found once encapsulated in the esophageal wall. A few specimens 108  
of Tetrarhynchus erinaceus were also found encapsulated in the  
esophageal wall. Some fish had a few specimens of Brachyphallus  
crenatus in their stomach, in addition to Derogenes varicus, and  
Tetrarhynchus quadrirostris was found in the body cavity of 3 salmon,  
Coenomorphus grossus in the body cavity of one salmon. The result  
of my examinations was therefore 9 parasitic species, all of them  
more or less numerous. Tetrabothrium minimum, the cestode larva  
discovered by VON LINSTOW, belongs here, too.

Except the purely potamophilous Ascaris aculeati, all species  
are either purely marine or marine-potamophilous. The Weser salmon  
carries all of them from the North Sea. Ascaris aculeati, <sup>an</sup> <sub>as</sub> 30  
encapsulated nematode, does not play an important part because the  
presumably free-swimming embryo can at any time enter the gullet  
with the respiratory water and through that can pass into the fish.

No remains of animal or plant nutrition were ever found  
anywhere in the entire digestive tract. It is therefore obvious that  
the Weser salmon, too, discontinues active feeding on its journey

through fresh water.

I can be brief in my report on the Elbe salmon, referring to the publications by FRITSCH (24) and to the biological and systematic chapters of this paper. The predominance of marine parasitic species indicates that the salmon does not feed in the Elbe. The only potamophilous-marine form (Echinorhynchus salmonis) probably entered the salmon when it descended through the brackish water of the river mouth, similar to the Baltic Sea salmon. FRITSCH proved that the salmon does not take in any food whatsoever as long as it is in the Elbe. Only during its descent it is sometimes so exhausted as to try and catch some food. The parasitic fauna reflects this starvation period.

Let us now consider the salmon of the two Scottish rivers, the Tay and the Tweed. From Tables VII and VIII we make the surprising discovery that both salmon species differ considerably in their behaviour from the standard so far established for the other North Sea salmon; their parasitic faunas rather resemble that of the Baltic Sea salmon. The Tweed salmon and even more the Tay salmon 109 show a high percentage of potamophilous elements; in the latter they even predominate.

McINTOSH's statements (64) on the parasitic fauna of the Tay salmon are incomplete and inaccurate inasmuch as the author

speaks of young salmon descending to the sea, then of salmon ascending the streams for spawning, and reports on parasites of one group and then the other rather inconsistently. He also does not give any details on the place where the examined salmon were caught, in the sea, in the lower or the upper course of the river.

Let us consider all parasites of the Tay salmon and the ways of infection. The salmon acquires the marine forms Derogenes varicus, Tetrabothrium minimum, Tetrarhynchus quadrirostris and Ascaris capsularia in the sea, presumably also Abothrium crassum (see chapter on systematics). Distomum spec., Tetrarhynchus spec. and Ascaris spec. also appear to be of marine origin. Echinorhynchus salmonis is a parasite which, as we have already seen in the cases of Baltic Sea and Elbe salmon, can infect fish in the sea and in fresh water. The same applies to Pomphorhynchus laevis. Only Azygia tereticollis can be acquired nowhere but in fresh water.

There is hardly an explanation for the predominance of potamophilous parasites in the salmon from the Scottish rivers. Perhaps a study of the water bodies into which these rivers fall might throw light on these strange parasitological findings. This would constitute a parallel to the Baltic Sea. Many English-Scottish rivers <sup>flow</sup> fall into the sea at the beginning of deep bays. These bays are small replicas of the large Baltic Sea: extensive

areas of brackish water where conditions are presumably similar to those in the Baltic Sea. The salmon ascending from the depths of the North Sea has ample opportunity to become infected with marine-potamophilous and potamophilous-marine parasites in these water bodies.

The parasitic fauna of the Tweed salmon shows that the above hypothesis is not totally unreasonable. Among the parasites of the Tweed salmon, there are only 2 potamophilous-marine species and, except Abothrium crassum, only one purely potamophilous species (Ascaris obtusocaudata). In the Tweed salmon, therefore, the marine 110 element dominates, contrary to the Tay salmon. Let us again turn to the manner in which the river falls into the sea for comparison and explanation of this phenomenon. The Tweed falls into the sea almost directly. There is no large area of brackish water between its mouth and the sea. Therefore the transition from sea to fresh water is much more abrupt than in the Tay; the parasitological boundaries are presumably much more clear-cut than in the Tay and the ascending salmon does not get an opportunity to acquire as many potamophilous-marine parasites as the Tay salmon.

This is one factor which might serve as an explanation for the high percentage of potamophilous parasites. The other factor, which I have already mentioned when discussing the Baltic Sea salmon, might be of equal significance. The gradual transition from

sea to fresh water may influence the nutritional habits of the ascending and descending salmon in the sense that the salmon occasionally take in food in fresh water, but mainly that the salmon after spawning, when descending to the sea, are much sooner able to take in food again. This is also indicated by the frequent instances when salmon were successfully caught on a fishing rod. I would like to emphasize, however, referring to the numerous tests by English and Scottish authors, that the ascending and descending salmon undergoes the same starvation period as the Rhine, Elbe, and Weser salmon. Proof for this starvation period are, in addition to the hundreds of salmon intestines which were found empty, the parasitological findings.

Nothing much remains to be said about the parasites themselves. They occur in similar numbers as in other salmon. A comparison of old and young salmon infected with Abothrium crassum, which was carried out by TOSH (99), is of considerable interest; it proves parasitologically what biological observations had made appear likely, namely that the starvation period of salmon is not related to the change of medium, but to their sexual life. In his review TOSH asks himself whether the decrease in the Abothrium crassum population towards autumn is constant and what is its cause. In my opinion, it is caused by the different timing of the starvation periods, i.e. by the <sup>time</sup> ~~difference~~ <sup>onset of the</sup> development of the genital organs. Fish which ascend the rivers at the beginning of that

development, that is in spring, still have a great number of 111  
parasites, especially Abothrium crassum. Fish ascending the rivers  
only in autumn with almost fully developed organs, have already  
undergone a starvation period in the sea, as HOEK has shown. There-  
fore they lost part of their parasites already in the sea. Another  
factor is perhaps the fact that during the winter months the fish  
are less eager to take in food. This, then, is the explanation for  
that phenomenon, and I think we can safely assume that it will be  
constant.

Like in Tay, Rhine, Elbe, North Sea and Loire salmon, the  
number of Abothrium crassum in a single Tweed salmon is always small.  
TOSH (99) summarizes the results of his examinations in the following  
sentence:

"Freshwater parasitic forms are very rare in the salmon,  
and the fact that they are practically absent in well grown fishes  
seems to point to the conclusion that salmon do not feed in the  
fresh water of a short river like the Tweed except under extra-  
ordinary conditions, when a prolonged stay is imposed upon them".

Thus TOSH found conditions similar to those reported by  
McINTOSH 40 years previously, and expresses them also in similar  
terms.

From the parasitic faunas of the Tweed and the Tay salmon,

which may be compared to that of the Baltic Sea salmon with regard to their composition, it appears that also the English-Scottish, ascending salmon do not deviate from the general standard. They also starve before spawning and for a considerable time afterwards, until the intestine has regenerated sufficiently (GULLAND) to be able to resume its digestive functions. If necessary, the descending salmon can take in food, but as a rule does so only after it has left the fresh water and is travelling towards the sea through the zone of brackish water.

Finally, let us compare the Pacific salmon with the Atlantic salmon. Unfortunately, the parasitic fauna of the Oncorhynchus species of North America, the salmon species of those regions, has been little studied as yet. Except in the publications by ZSCHOKKE and HEITZ (116), hardly any definite specific names are given. 112

Only Abothrium crassum is mentioned by the other authors, which unfortunately is the very parasite which lends its host the least distinct parasitological profile. In addition to this very common salmonid cestode, Ascaris capsularia, Coenomorphus grossus, Tetra-rhynchus quadrirostris and Bothriocephala larvae also parasitize the various Oncorhynchus species. The Acanthocephala are represented by 2 marine species. Trematodes are absent, at least they are unknown. WARD's statements in this respect are still very uncertain. Of purely potamophilous parasites, we know only ectoparasites

(Copepods) and Henneguya Zschokkei. Pelichnibothrium caudatum, a marine cestode, also seems to occur quite frequently.

We see that little is known about the fauna, but from these findings as well as from the descriptions by McMURRICH (65), MILNE (67), and from WARD's paper which supplies considerable information, we can reconstruct a certain picture. According to WARD's observations (102), Oncorhynchus nerca feeds voraciously in the sea, but does not take any food in fresh water. After spawning, most of the fish die. The population of endoparasites did not change much during the journey of the salmon, either. Only Abothrium crassum disappeared completely in fresh water, which, however, could be explained by the rare occurrence of this cestode. After the fish have died, all parasites leave the intestine. No more endoparasites of potamo-philous origin entered the fish; only large numbers of ectoparasites attached themselves to the gills and the skin - similar to the Rhine and Elbe salmon.

It seems to be due to the low rate of infection and the long journey that Oncorhynchus nerca from the upper course of the river has no more cestodes. Rhine salmon often has many of those cestodes in the lower course of the river, and in the upper course, hardly 1,000 km higher upstream, only few specimens or remains are left or they are entirely missing.

All this shows that first the behaviour of the parasites

in Oncorhynchus nerca does not differ as much from that of the Rhine salmon as WARD had assumed. Both lose their parasites gradually, one more slowly than the other; after all, this varies even among Rhine salmon. Both retain their body cavity parasites, 113 as is to be expected. Also, both have only purely marine parasites while ascending. During their entire journey to the spawning grounds they do not take in any freshwater parasites. While the Oncorhynchus species die, however, from exhaustion after their long journey, the Atlantic salmon has the opportunity to take in purely potamophilous parasites while descending to the sea.

WARD's observations agree completely with those made on the salmon from Kamtchatka, and the above statements apply therefore fully to that Asiatic salmon, too. From the composition of the parasitic fauna and the origin of the individual parasitic species, ZSCHOKKE and HEITZ (116) have demonstrated that the Oncorhynchus species of Kamtchatka must be very similar, too, to Salmo salar from the Atlantic Ocean and from the European rivers. The parasitic fauna of the Oncorhynchus species from Kamtchatka consists of only a few species: 9, of which 5 are cestodes, 1 a nematode, 2 acanthocephalans, and 1 myxosporidian. Of these 9, 7 are purely or almost purely marine; only Abothrium crassum and the myxosporidian Henneguya Zschokkei are potamophilous. There are also very few mature forms (2: Abothrium crassum and Echinorhynchus gadi) and intestinal parasites among the parasites. This, again, is in agreement

with conditions in the European salmon. "The composition and character of the parasitic fauna of Oncorhynchus is explained by the habits of the fish, its single journey upstream, and its starvation period in the river"(116).

In concluding, let us consider briefly the parasitological results obtained by WARD (103) when examining the purely potamophilous salmon species Salmo salar sebago from Lake Sebago in North America. They cannot be compared with any of the European salmon discussed in the course of this chapter. They come closest to conditions in the Baltic Sea salmon. A parallel can perhaps be drawn to the salmon which allegedly have become inhabitants of the vast Russian and Swedish lakes and reportedly do not descend to the sea any more, like the sebago salmon. Unfortunately we do not have any parasitological 114 details on those freshwater salmon, but we may assume that their faunas are purely potamophilous, too.

As I have already set out in detail in the chapter on systematics, Salmo salar sebago has a purely potamophilous parasitic fauna consisting of various cestodes and cestode larvae, one trematode and several nematodes which, however, <sup>have</sup> not yet been clearly identified. WARD suspects at least one form to be of marine origin: an interesting parallel to the cases mentioned by ZSCHOKKE (115) from Silurus glanis and Lota vulgaris. Abothrium crassum is most common because living conditions were highly favourable for it: the more purely

potamophilous salmonid, the higher its rate of infection by this cestode. Baltic Sea salmon are more strongly infected by it than North Sea salmon, marine trout more strongly than Baltic Sea salmon, and the highest rate of infection, as becomes obvious from WARD's figures, is found in sebago salmon.

Its purely potamophilous parasitic fauna is due to its living habits - it does not migrate to the sea any more, but stays in fresh water all its life, has stayed there for generations, and has adapted itself completely.

WARD (103) concludes his observations with the following sentence which has my full agreement:

"The parasitic fauna of any animal (here specially of the sebago salmon) is the product of its habitat".

### 3. The parasitic fauna of some other migratory fish

After having dealt with salmon and their parasites, let us have a look at some other migratory fish to see whether we find agreement of habitat and parasitic fauna in them, too. Already ZSCHOKKE (112) pointed out that in other migratory fish, too, the composition of the parasitic fauna was the reflection of their living habits. On the basis of more recent studies and observations, I would like to advance along the same lines as ZSCHOKKE.

Nutrition and parasitic fauna of the following migratory fish shall be discussed briefly below: 115

<u>Salmo trutta</u>	<u>Anguilla vulgaris</u>
<u>Osmerus eperlanus</u>	<u>Petromyzon fluviatilis</u>
<u>Coregonus oxyrhynchus</u>	<u>Acipenser sturio</u>
<u>Alosa vulgaris</u>	

Together, these 7 migratory fish (Salmo salar and its parasitic fauna excluded) carry 112 parasitic species, of which 18 are cestodes, 41 trematodes, 36 nematodes, and 17 acanthocephalans. They may be divided into the following groups on the basis of their origin:

Marine		35	}	45
	(predominantly marine	( 10	)	
Marine-potamophilous	(	19	(	
	(predominantly potamophilous	( 9	)	
Potamophilous		25	)	34
Specific forms				<u>33</u>
				112

The majority of parasites of migratory fish are trematodes and, purely marine, a fact which is of even greater significance for our purposes. There are, however, a considerable number of freshwater parasites, too. Those forms are fewest which can parasitize fish both in sea and fresh water. 116

Table IX

Wander- fische: A	○	○×	○	×C	×	×	B eigen:	C	D	Anzahl d. Arten (Zschok- ke) 1891
<i>Acipenser sturio.</i>	8	4	12 = 70,58 %	4	1	2 = 11,76 %	3 = 17,64 %	17	12	
<i>Alosa vulgaris.</i>	7	2	9 = 60,23 %	1	1	1 = 7,69 %	3 = 23,07 %	13	10	
<i>Anguilla vulgaris.</i>	22	7	29 = 50,87 %	7	10	17 = 29,32 %	11 = 19,29 %	57	38	
<i>Salmo salar</i>	18	6	24 = 39,34 %	7	10	17 = 27,86 %	20 = 32,78 %	61	33	
<i>Osmerus eperlanus.</i>	5	2	7 = 26,92 %	3	8	11 = 42,30 %	8 = 30,76 %	26	21	
<i>Salmo trutta.</i>	3	1	4 = 19,04 %	8	8	16 = 76,19 %	1 = 4,76 %	21	16	
<i>Coregonus oxyrhynch.</i>	1	1	2 = 18,18 %	2	0	8 = 72,72 %	1 = 9,09 %	11	10	
<i>Petromyzon fluviatilis.</i>	1	1	2 = 22,22 %	1	1	1 = 11,11 %	6 = 66,66 %	9	8	

A - migratory fish

B - specific

C - number of species

D - number of species (ZSCHOKKE)

1891

In Table IX I tried to summarize the parasitic faunas of several migratory fish. I included Salmo salar for purposes of comparison. One glance at this Table shows that in some migratory fish the marine element dominates, in others the potamophilous element. To make matters even clearer, I have added another table in which all specific forms have been omitted, and the mainly marine parasites have been included in the purely marine species, the mainly potamophilous in the purely potamophilous species. We get the following results (Table X).

I would, however, like to mention in connection with this Table that the impression it gives is only partly correct because, for one thing, all specific forms have been omitted the nature of

which would have to be studied, assigning the individual forms to their respective species, and for another, the parasitic faunas of all migratory fish listed would have to be studied as carefully and thoroughly as that of Salmo salar in this paper.

Table X

A Wanderfische:	B marine Arten	C potamoph. Arten:	D Total:
<i>Alosa vulgaris.</i>	9 = 90,0 %	1 = 10,0 %	10
<i>Acipenser sturio.</i>	12 = 85,7 %	2 = 14,3 %	14
<i>Petromyzon fluviatilis.</i>	2 = 66,7 %	1 = 33,3 %	3
<i>Anguilla vulgaris.</i>	29 = 63,0 %	17 = 37,0 %	46
<i>Salmo salar</i> (ohne Ectoparasit.) <sup>E</sup>	22 = 62,9 %	13 = 37,1 %	35
<i>Osmerus eperlanus.</i>	7 = 41,2 %	10 = 58,8 %	17
<i>Salmo trutta.</i>	4 = 20,0 %	16 = 80,0 %	20
<i>Coregonus oxyrinchus.</i>	2 = 20,0 %	8 = 80,0 %	10

A - migratory fish                      B - marine species  
C - potamophilous species      D - total  
E - (without ectoparasites)

Apart from Salmo salar, Anguilla vulgaris has undoubtedly the most interesting living habits, development and nutrition. It migrates to the sea to spawn and presumably dies there after spawning. The young eel, or elvers, still undergoing metamorphoses, ascend from the depths of the sea to the coastal waters. They are said to refrain from feeding during that period. Not before reaching 117 fresh water does the young eel start taking in food, first plancton and terrestrial forms, later also young fish and frequently even the eggs of other freshwater fish. The eel remains in fresh water 5-8 years and feeds there. Upon maturity it descends to the sea again, without feeding, to spawn there in great depths. More recent

studies have shown that large numbers of elvers remain at the coast and in mouths of rivers, while the others ascend the streams. Those which remain are mainly males which feed on marine animals of all types and wait until the females descend the streams. Together they migrate then to the spawning grounds. We have, therefore, 2 groups of eels which live in completely different habitats.

What is the relation between parasitic fauna and nutrition in these animals? Looking at the figures in Tables IX and X, we see immediately that their parasitic fauna consists of almost equal numbers of marine and potamophilous species. Contrary to Salmo salar, freshwater elements are strongly represented which indicates feeding in that medium. Comparing the statements made further above on the nutritional habits of the eel with the figures of the Tables, we notice that there is agreement in many respects; we may assume that the males remaining in the sea would have rather marine and possibly marine-potamophilous parasites, while the females become infected in fresh water with purely potamophilous and potamophilous-marine species. This, therefore, is an exact mirror image of the living habits of the eel and a distinct indication of the various habitats it frequents.

Let us now consider the other migratory fish, first Alosa vulgaris. BARFURTH (4), WEBER (105) and HOEK (40) have studied the nutritional habits of this fish. They examined the stomach contents

of old and young shads and obtained the following interesting results: The descending young shads feed on insects and small crustaceans. The old ascending fish which migrate to their spawning grounds, however, have often only a mucous plug in their stomachs which contains remains of food inside, mostly remains of the brackish water form Temorella affinis. When entering the mouth of the river, the fish still feed, but on their way upstream they do 118 not feed at all. Exhausted from their journey which <sup>never</sup> takes them far upstream, and from spawning, they return to the sea, emaciated.

Let us again compare these findings with the figures on the parasitic fauna of Alosa vulgaris in Tables IX and X. Again we find full agreement between nutrition and parasitic fauna. The marine element predominates. On account of its starvation period in fresh water Alosa vulgaris does not have an opportunity to become infected with potamophilous parasites. Another contributive factor is the fact that the shads never travel far upstream; according to HOEK, they often hardly leave the brackish water region.

Again, biological and parasitological observations agree with each other.

Unfortunately we know little as yet on the nutrition of Acipenser sturio and Petromyzon fluviatilis. Presumably they both feed on small animals in the sea; in fresh water, on the other hand, during their migration to their spawning grounds, they take in very

little food. Petromyzon fluviatilis which leads partly a parasitic life, has a very specific parasitic fauna; as can be seen from Table IX. In Acipenser sturio the marine elements dominate.

Now to the closest relatives of the salmon, Osmerus eperlanus, Coregonus oxyrhynchus and Salmo trutta. They are the exact opposite of all migratory fish so far mentioned with regard to nutrition.

Osmerus eperlanus and Coregonus oxyrhynchus prefer the Baltic Sea. Both migrate into the coastal rivers falling into the Baltic Sea to spawn and there feed in the same manner as in the sea. These living habits naturally determined also the population and the character of the parasitic fauna, and in both fish the potamophilous element is in fact stronger than the marine element. Another factor may contribute to this phenomenon, namely, that both fish species live in the Baltic Sea which has repeatedly been classified as very favourable for the adaptation of potamophilous species. Osmerus eperlanus and Coregonus oxyrhynchus can therefore become infected with potamophilous parasites already in the brackish water region. 119 It should also be pointed out that Coregonus oxyrhynchus can adapt itself very easily to purely freshwater conditions.

Again, in these migratory fish from the Baltic Sea, far-reaching agreement between living habits and parasitic fauna.

Salmo trutta, finally, leads a life similar to that

of the two above-mentioned fish. Unfortunately we are not entirely familiar with the living habits of marine trout. Systematically, it stands between the purely potamophilous brook trout and the migratory fish Salmo salar, and also with regard to its living habits, so that the opinion has been repeatedly voiced that the marine trout could perhaps be a hybrid of the two fish species.

In the sea the marine trout feeds as much as the salmon and discontinues feeding only with the commencement of maturity which can already set in in the sea. It starves while it migrates in fresh water. After spawning it feeds again and slowly descends to the sea. According to GIARD (26,27), the marine trout stays in the sea as long as the salmon.

Let us compare the above with the parasitic fauna of the marine trout. Immediately we notice that the purely potamophilous and potamophilous-marine element dominates. When discontinuing feeding, the marine trout presumably loses its marine parasites which it carried from the sea. After spawning, however, it proves to be a voracious predatory fish (the nature of trout) and therefore becomes infected with a large number of potamophilous parasites. It is interesting to note that of its 17 parasitic species, as many as 12 are found also in Salmo fario.

From what we know today about the parasitic fauna and living habits of the marine trout, they also agree.

From these few examples on the relationship between nutrition and living habits, on the one hand, and parasitic fauna, on the other hand, it becomes apparent that we can draw conclusions from the nutrition biology of an animal on its parasitic fauna and vice versa: from the parasitic fauna of an animal, its character and its composition we can draw conclusions on the living habits, habitat and nutrition of that animal.

This manifests itself most clearly in migratory fish. 120  
Their parasitic fauna follows the same pattern as their living habits which are completely determined by their sexual life. If some fish starve in the sea, they do not have any marine parasites (the female eels), if some starve in fresh water they do not have any potamophilous species at all (Petromyzon fluviatilis) or only very few (Salmo salar). If they, however, feed both in the sea and in the fresh water; their parasitic fauna, depending on the place the fish is caught, contains either marine or potamophilous parasites (Salmo trutta, Coregonus oxyrhynchus, Osmerus eperlanus).

IV. Geographical Part

In 1896, ORTMANN (80) made the following comments on the geographical distribution of these worms, in particular the parasitic forms: "Our systematic knowledge of this group of animals (parasites) is still very inadequate, and our knowledge on their geographical distribution is non-existent".

Even today, 20 years later, our knowledge in this respect has not widened much. Although abundant geographical findings are accumulated in numerous parasitological works, no or very few attempts have been made so far to carry out comprehensive studies on one or the other group of parasites. Exceptions are of course the pathogenic parasites of man and those animals which are useful to man. Their distribution and frequency has been studied extensively for sanitary reasons.

Even in this paper it is impossible to carry out a thorough study of the geographical distribution of fish parasites, as on the one hand such studies would be too far-reaching, and on the other hand the subject is too great and too difficult to be treated, as it were, as a supplement to a parasitological-biological paper of completely different contents. Research into the geographical distribution of these parasites meets with great difficulties, partly obstacles which cannot be removed with our present knowledge.

of the life of many of these parasites. The life cycle of most of them is not known at all or only in fragments. We know their hosts or the intermediate host(s); of many parasites we <sup>know</sup> only/one or the other. We do not know how many hosts or intermediate hosts certain parasites have; we do not know whether it undergoes a free stage, thereby being exposed to extraneous influences, or whether it is permanently attached to its host. We also know very few of the possibilities of spreading, both active and passive, of which there are surely a great number.

Below, I would like to discuss the geographical distribution and the possibilities of distribution of some salmon parasites.

On account of their mostly inactive life, all parasites are attached to their hosts or intermediate hosts. We must therefore study the geographical distribution of these hosts. In the chapter on systematics, I have divided the parasites on the basis of this fact by classifying them into purely marine, marine-potamophilous, potamophilous-marine and purely potamophilous species, depending on whether they parasitize predominantly ~~in~~ marine fish or freshwater fish or only ~~in~~ one or the other. From the various lists of hosts we see which fish, how many fish, and, particularly, which migratory fish the individual parasitic species parasitize. The various tables with the data on the various localities also show where the respective parasites are found and what is the scope of their horizontal range of distribution.

Table XI

Districts	Zone	Subregion	Localities	Parasites
Mariner Lebensbezirk: Marine	Arctic	arktisch-circumpolare	A Nördliches Eismeer, Murmanküste, Grönland.	<i>Derogenes varicus</i> , <i>Lecithaster gibbosus</i> , <i>Brachyphallus crenatus</i> ; <i>Abothrium crassum</i> ; <i>Ascaris adunca</i> , <i>Ascaris clavata</i> , <i>Asc. communis</i> , <i>Asc. capsularia</i> , <i>Asc. angulata</i> ; <i>Echinorhynchus gadi</i> , <i>Acanthocephalus lucii</i> ; <i>Pomphorhynchus laevis</i> .
		atlantisch-boreale	B Norwegische Küste; Ostsee; Nordsee; Küste von Irland, Belgien, Frankreich, Portugal.	<i>Derog. varicus</i> , <i>Lecith. gibbosus</i> , <i>Brachyph. crenatus</i> ; <i>Abothr. crassum</i> , <i>Scolex pleuronectis</i> ; <i>Ascaris adunca</i> , <i>Asc. clavata</i> , <i>Asc. communis</i> , <i>Asc. angulata</i> , <i>Asc. capsularia</i> ; <i>Echinorhynch. heteracanthis</i> , <i>Ech. gadi</i> , <i>Ech. truttae</i> , <i>Ech. salmonis</i> , <i>Pomphorhynch. laevis</i> , <i>Acanthoceph. lucii</i> . <sup>Spread:</sup> Verschleppt: <i>Ascaris acuta</i> , <i>Ech. agilis</i> .
		arktisch-boreale	C Bering-See; Küste v. Alaska, Ostküste von Kamtschatka.	<i>Abothrium crassum</i> ; <i>Ascaris communis</i> , <i>Asc. capsularia</i> ; <i>Ech. truttae</i> , <i>Ech. gadi</i> .
circum-tropische	Arctic	pacifisch-boreale	C Bering-See; Küste v. Alaska, Ostküste von Kamtschatka.	<i>Abothrium crassum</i> ; <i>Ascaris communis</i> , <i>Asc. capsularia</i> ; <i>Ech. truttae</i> , <i>Ech. gadi</i> .
		mediterrane	D Adriat., Tyrrhenisches Meer, Ligurische Küste, Küste von Sardinien.	<i>Scolex pleuronectis</i> ; <i>Brach. crenatus</i> ; <i>Ascaris adunca</i> , <i>Asc. communis</i> , <i>Asc. acuta</i> , <i>Asc. clavata</i> , <i>Asc. capsularia</i> ; <i>Acanthocephalus lucii</i> , <i>Necorhynchus agilis</i> . <sup>Spread:</sup> Verschleppt: <i>Triacnophorus nodulosus</i> ; <i>Cucullanus elegans</i> ; <i>Pomphorhynch. laevis</i> .
ant-arktische	Antarctic	arktische	E Feuerland, Chile.	<i>Ascaris capsularia</i> , <i>Asc. adunca</i> .
		European-Asiatic	F Schwed. u. Ostpreuß. Seenplatte; Onegasee; Plönersee; See in Turkestan, Baikalsee; Flußgebiete des Ob, Jenissei, Elbe, Weser, Ems, Rhein, Loire, Rhone, Po, Tiber, Donau; russ. Zuflüsse des Schwarz. Meeres.	<i>Crepidostomum farionis</i> , <i>Azygia tetricollis</i> ; <i>Abothr. crassum</i> , <i>Schistocephalus gasterostei</i> , <i>Triacnoph. nodulosus</i> ; <i>Ascaris aculeati</i> , <i>Asc. obtusocaudati</i> , <i>Cuc. elegans</i> ; <i>Acanth. lucii</i> , <i>Pomphorhynch. laevis</i> , <i>Necorhynchus rutili</i> , <i>Ech. truttae</i> , <i>Ech. salmonis</i> . <sup>Spread:</sup> Verschleppt: <i>Brach. crenatus</i> , <i>Lec. gibbosus</i> , <i>Derog. varicus</i> ; <i>Scolex pleuronectis</i> ; <i>Ascaris capsularia</i> , <i>Asc. adunca</i> , <i>Asc. clavata</i> , <i>Asc. communis</i> , <i>Asc. angulata</i> ; <i>Ech. heteracanthis</i> , <i>Ech. gadi</i> , <i>Necorhynch. agilis</i> .
Süßwasser-Lebensbezirk: Freshwater	northern-moderate	nördliche-gemäßigte	F Elbe, Weser, Ems, Rhein, Loire, Rhone, Po, Tiber, Donau; russ. Zuflüsse des Schwarz. Meeres.	<i>Crepidostomum farionis</i> , <i>Azygia tetricollis</i> ; <i>Abothr. crassum</i> , <i>Schistocephalus gasterostei</i> , <i>Triacnoph. nodulosus</i> ; <i>Ascaris aculeati</i> , <i>Asc. obtusocaudati</i> , <i>Cuc. elegans</i> ; <i>Acanth. lucii</i> , <i>Pomphorhynch. laevis</i> , <i>Necorhynchus rutili</i> , <i>Ech. truttae</i> , <i>Ech. salmonis</i> . <sup>Spread:</sup> Verschleppt: <i>Brach. crenatus</i> , <i>Lec. gibbosus</i> , <i>Derog. varicus</i> ; <i>Scolex pleuronectis</i> ; <i>Ascaris capsularia</i> , <i>Asc. adunca</i> , <i>Asc. clavata</i> , <i>Asc. communis</i> , <i>Asc. angulata</i> ; <i>Ech. heteracanthis</i> , <i>Ech. gadi</i> , <i>Necorhynch. agilis</i> .
		nord-amerikanische	G Vereinigt. Staaten, Alaska, Grönland.	<i>Azygia tetricollis</i> ; <i>Abothrium crassum</i> , <i>Schistocephalus gasterostei</i> .

- A - Arctic Sea, coast of Murmansk, Greenland  
 B - Norwegian coast; Baltic Sea; North Sea; coasts of Ireland, Belgium, France, Portugal, eastern coast of the United States, of Canada  
 C - Bering Sea; coast of Alaska, east coast of Kamtschatka.  
 D - Adriatic and Tyrrhenian Seas, Ligurian coast, Sardinian coast.  
 E - Tierra del Fuego, Chile.  
 F - Flat country lakes in Sweden and East Prussia; Lake Onega; Plön Lake; lake in Turkestan, Lake Baikal; river basins of the Ob, Yenisey, Elbe, Weser, Ems, Rhine, Loire, Rhone, Po, Tiber, Danube; Russian tributaries of the Black Sea.  
 G - United States, Alaska, Greenland.

These two points, horizontal distribution and the number and species of hosts, have been elaborated in two Tables summarizing the data contained in the various lists of hosts.

Table XI is based on ORTMANN's (80) zoogeographical classification. We are concerned only with the following regions: all subregions of the Arctic zone, only the mediterranean subregion, comprising the Mediterranean, of the circumtropical zone, and only the southernmost local fauna of South America of the Antarctic zone.

From this Table we can see at a glance which parasites are typical for any given region, but another point is of even greater importance to us. We find that in each subregion (except in the Arctic one) parasites occur which are completely foreign to the area concerned. Responsible for this circumstance are not only the fish with a wide distribution, but particularly migratory fish. On their journeys in salt or fresh water they can spread the 123 parasite to completely different parts of the sea or river basins. They mainly carry marine parasites into fresh water and potamophilous species into salt water. Neorhynchus agilis, for instance, is a typical parasite of Mediterranean fish. Through marine fish it must have been spread to the Atlantic Ocean, and Salmo salar even takes it as far as the Rhine. Migratory fish also carry a fair number of purely potamophilous parasites to the sea. Complete acclimatization, however, does not take place at all or very rarely, even if the

repeatedly particular parasite is/carried into the foreign medium (although Salmo salar carries Derogenes varicus in large numbers into fresh water, no freshwater fish has ever been found infected with it). ZSCHOKKE (115) reports on several cases of acclimatization (Tetra-rhynchus erinaceus and Ascaris capsularia). FRITSCH's (24) report on the infection of Elbe fish by Scolex pleuronectis can likewise be interpreted as an acclimatization of the parasite to fresh water, although perhaps only temporarily. Usually, parasites die in a medium foreign to them, if they do not leave their hosts, like the ectoparasites, before the latter enter a different medium.

The above, however, applies only to the acclimatization of parasites to localities far away from their usual habitats, so that only pure migratory fish which regularly travel from one medium to the other, can be considered to spread the parasites.

Conditions are different in the transitional zone between freshwater and sea, in brackish water. There, an exchange of marine and potamophilous parasites is nothing unusual, and we might even speak of a parasitic fauna of brackish water. One part of that fauna is contributed by marine fish, the other part by freshwater fish. Of course migratory fish again play the main part in spreading the parasites, but many other fish also enter that region, either in search of food or to spawn. All of them carry parasites into brackish water, freshwater fish potamophilous species, marine fish

marine species. Parasites which leave their hosts become acclimatized to brackish water if they find suitable hosts or intermediate 124 hosts, and when feeding both marine and potamophilous fish may become infected with parasites which are totally foreign to their specific parasitic fauna. There is of course the more opportunity for such an infection the larger the area of brackish water is and the more slowly the transition from fresh water to salt water is made. As I have already demonstrated in the systematic part and especially in the faunistic part, the Baltic Sea is a vast body of brackish water. Therefore we find there the greatest exchange of marine and potamophilous faunal elements. Especially in the eastern part of the Baltic Sea, this intermingling of species is almost the rule. In the East Prussian lagoons and the Finnish reefbelt, we find both purely freshwater and purely marine fish, also a large number of migratory fish of which in particular 2, Osmerus eperlanus and Coregonus oxyrhynchus, are almost typical of the Baltic Sea. They all contribute to the possible acclimatization of one or the other species to brackish water. This, however, completely blurs the zoogeographical boundaries which hold true for marine and potamophilous parasites elsewhere. Not only do marine fish take freshwater elements to the sea from there and freshwater fish marine elements far inland, but also the migratory fish acquire the elements foreign to their parasitic fauna and carry them into fresh or salt water. Salmon which, as we now know, do not feed in fresh water and therefore

do not acquire parasites, or only very rarely, become infected with potamophilous parasites, if not in fresh water, so very likely in brackish water, either on their return from the streams or perhaps while they gather in front of the mouth of the river to set out on their journey upstream.

Intermediate hosts naturally play an important part in the acclimatization of a parasite in a certain area. To the extent such hosts are available, thus providing a suitable nutritive medium for the parasite, the latter can become acclimatized to a foreign habitat. This is again very difficult in localities at a great distance from the natural habitat of the parasite, and very easy in 125 localities where the two habitats meet. Here again the Baltic Sea provides the most favourable conditions, and we find all marine-potamophilous or potamophilous-marine salmon parasites there. The latter element dominates in the Baltic (5 species, 4 of them acanthocephalans, compared to 3 species); in the North Sea, on the other hand, we find more marine-potamophilous species (4 compared to 2), that is species introduced from the sea.

It is therefore obvious that the distribution of the parasite is closely linked with the distribution of hosts and intermediate hosts. If the latter are missing, the parasite cannot become acclimatized in a foreign habitat. Ascaris acuta and Neorhynchus agilis are above all representatives of the parasitic

fauna of the Mediterranean. This is presumably due to the high salt content of that water body. The intermediate hosts cannot live in seas with lower salt content and thereby the distribution of the parasites in their larval stages is limited. As mature worms these two species, as we have seen, can be carried to far-away localities and occasionally even into fresh water by migratory fish. In the Baltic Sea salmon the Rhynchobothria larvae are mostly missing because their hosts, in particular the Selachii, do not come to the Baltic Sea. Freshwater fish which live far away from the sea do not have any marine parasites (apart from the few exceptions already mentioned above).

If a parasite is widely distributed, however, we may with fair certainty take this to be an indication for a wide distribution of their hosts and intermediate hosts. Calliobothrium filicolle with its larva Scolex pleuronectis, and Pomphorhynchus laevis take their hosts and intermediate hosts especially from among fish which by their natural, more or less wide distribution provide for a wide distribution of their parasites, too. Abothrium crassum can be found in all water bodies of the Arctic and moderate zones of the northern hemisphere, like its hosts, the Salmonidae. It is an interesting fact that the parasites spread mainly from east to west and from west to east, rarely from north to south and vice versa. This is easily explained by the fact that on the same latitudes the living conditions

Table XII

Number of fish infected with salmon parasites ←	Anzahl der mit Lachsparasiten infizierten Fische.	Meerfische: Marine fish					Wanderfische: Migratory fish					Süßwasserfische: Freshwater fish					
		1-4	5-10	11-20	21-40	Total	1-4	5-10	11-20	21-40	Total	1-4	5-10	11-20	21-40	Total	
I. <i>Cyclostomatus</i> :	1	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—
II. <i>Salachei</i> :	26	26	—	—	—	26	—	—	—	—	—	—	—	—	—	—	—
III. <i>Gunoidei</i> :	4	—	—	—	—	—	3	1	—	—	—	4	—	—	—	—	—
IV. <i>Teleostei</i> :																	
1. <i>Acanthopterygii</i> :	135	117	7	1	—	125	2	—	1	—	3	5	2	—	—	—	7
2. <i>Pharyngognathi</i> :	6	6	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—
3. <i>Anacanthini</i> :	67	51	13	—	—	64	—	—	—	—	—	1	2	—	—	—	3
4. <i>Cypriniformi</i> :	107	23	2	1	—	26	4	4	2	1	11	62	8	—	—	—	70
5. <i>Lophobranchii</i> :	4	4	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—
6. <i>Plectognathi</i> :	5	5	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—
	355	232	22	2	—	256	10	5	3	1	19	68	12	—	—	—	80

are more or less the same and therefore also the hosts and intermediate hosts. Typical examples are the distribution of Abothrium crassum and the distribution of Derogenes varicus, both of which live only in the Arctic and moderate zones, but occur on the European and North American coasts.

Let us also consider briefly the distribution of salmon parasites in hosts or intermediate hosts. Table XII informs us of the number and species of the marine, migratory and freshwater fish

in which salmon parasites have been found.

According to the Table, 355 fish were infected, of which 256 were marine, 19 migratory and 80 freshwater fish. This composition shows again that Salmo salar has parasitic species which mostly parasitize marine fish, too, which is indirect proof that the parasitic fauna of salmon is more marine than photamophilous. The Teleostei easily have the highest rate of infection, several classes of which have numerous parasite carriers - the Acanthopterygii (percids, mullids, sparids, sciaenids, etc.), the Anacanthini (gadids, pleuronectids, etc.) and the Physostomi (salmonids, cypriids, esocids, etc.). The rate of infection in the ganoids and Selachii, on the other hand, is low.

Among the Physostomi are those fish which have most of the parasites in common with Salmo salar, above all Clupea harengus with 12 species, Salmo trutta and Anguilla vulgaris with 14 species each, Gasterosteus aculeatus from the class of the Acanthopterygii has 12 salmon parasites. The distribution and rate of infection of parasites in the individual families can be seen from the various lists of hosts in the chapter on systematics, and from the above Table. The figures 1-4, 5-10, 11-20, 21-40, refer to the number of salmon parasites found. The figures in the columns refer to the number of fish which may be infected with the above-mentioned

numbers of parasites, for instance: 26 Selachii were found infected by 1-4 salmon parasites, or: of migratory Physostomi, 4 are infected with 1-4, 4 with 5-10, 2 with 11-20, and 1 with 21-40 salmon parasites.

V. Summary of results

(1) From previous studies and this author's own examinations, the list of parasites of Salmo salar was drawn up as follows:

Table XIII.

(2) Table XIV provides information on the origin of salmon parasites (purely marine, marine-potamophilous, and purely potamophilous).

(3) The following parasites are:

(a) new in Salmo salar: Tetrarhynchus erinaceus v.BEN.

(b) new in Rhine salmon: Lecithaster gibbosus (RUD.),  
Azygia tereticollis (RUD.), Crepidostomum farionis (MÜLL.);  
Scolex pleuronectis MÜLL.

(c) new species for science (found in Rhine salmon): Tetra-  
bothrium spec. HEITZ, Echinorhynchus heteracanthis HEITZ.

(4) The nature of the intestinal parasitic fauna changes with the change of medium. Only parasites enclosed in the body cavity and in compact organs remain the same. The longer the salmon stays in the river, the less numerous in species and individuals the fauna of intestinal parasites becomes. The intestinal parasitic fauna of Salmo salar reflects its habitats.

(5) Salmon living mainly in the sea have purely marine, marine-potamophilous and very rarely potamophilous-marine parasitic species.

Purely potamophilous parasites, on the other hand, indicate life in fresh water (sebago salmon).

(6) The ascending salmon loses its marine parasites. The descending salmon has no or very few marine forms.

Table XIII

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Endoparasites.	Nemathelminthes:
Plathelminthes.	Nematodes:
Trematodes:	32. <i>Ascaris clavata</i> RUD.
1. <i>Deroogenes varicus</i> (MÜLL.).	33. <i>Ascaris adunca</i> RUD.
2. <i>Brachyphallus crenotus</i> (RUD.).	34. <i>Ascaris acuta</i> MÜLL.
3. <i>Hemiurus Lüheii</i> (ODD.).	35. <i>Ascaris ongidata</i> RUD.
4. <i>Hemiurus appendiculatus</i> (RUD.).	36. <i>Ascaris obtusocaulata</i> ZED.
5. <i>Distomum reflexum</i> ZSCHÖPKE nec. CREPLIN.	37. <i>Ascaris aculeati</i> v. LINST.
6. <i>Distomum Miescheri</i> ZSCHÖPKE.	38. <i>Ascaris capsularia</i> RUD.
7. <i>Distomum spec.</i> Mc. INTOSH.	39. <i>Ascaris communis</i> DIES.
8. <i>Sinistrophorus simplex</i> (RUD.).	40. <i>Ascaris spec.</i> Mc. INT.
9. <i>Lecithaster gibbosus</i> (RUD.).	41. <i>Ascaris spec.</i> LINTON.
10. <i>Azygia tereticollis</i> (RUD.).	42. <i>Ascaris spec. I.</i> ZSCHÖPKE.
11. <i>Crepidostomum farionis</i> (MÜLL.).	43. <i>Ascaris spec. II.</i> ZSCHÖPKE.
Cestodes:	44. <i>Ascaris spec.</i> HEITZ.
12. <i>Bothrium crossum</i> (BLOCH).	45. <i>Cucullanus elegans</i> ZED.
13. <i>Bothriocephalus osmeri</i> v. LINST.	Acanthocephala:
14. <i>Bothriocephalus spec. I.</i> larva ZSCHÖPKE.	46. <i>Neorhynchus rutili</i> (MÜLL.).
15. <i>Bothriocephalus spec. II.</i> larva ZSCHÖPKE.	47. <i>Neorhynchus agilis</i> (RUD.).
16. <i>Bothriocephalus spec. III.</i> larva ZSCHÖPKE.	48. <i>Acanthocephalus lurii</i> (MÜLL.).
17. <i>Bothriocephalenteron</i> ZSCHÖPKE.	49. <i>Echinorhynchus gadi</i> (MÜLL.).
18. <i>Bothriocephalus spec.</i> HASSALL.	50. <i>Echinorhynchus truttiae</i> SCHRANK.
19. <i>Taenia spec.</i> larva TOSH.	51. <i>Echinorhynchus salmonis</i> MÜLL.
20. <i>Tetrabothrium minimum</i> v. LINST.	52. <i>Echinorhynchus heteracanthis</i> HEITZ.
21. <i>Tetrabothrium spec.</i> larva HEITZ.	53. <i>Echinorhynchus spec.</i> SCHNEID.
22. <i>Tetrabothrium spec.</i> larva HEITZ.	54. <i>Echinorhynchus spec.</i> ZSCHÖPKE.
23. <i>Triacnaphorus nodulosus</i> (PALL.).	55. <i>Pomphorhynchus laccis</i> (ZORCA).
24. <i>Schistocephalus gasterostei</i> (FABR.).	Ectoparasites.
25. <i>Scolex pleuronectis</i> MÜLL.	Copepods:
26. <i>Coenomorphus grossus</i> (RUD.).	56. <i>Lepocephirus Strömii</i> BAIRD.
27. <i>Tetrarhynchus quadrivestris</i> (GZE.).	57. <i>Lernaeopoda salmonica</i> LIN.
28. <i>Tetrarhynchus erinaceus</i> v. BEN.	58. <i>Lernaeopoda corpiensis</i> KRAEY.
29. <i>Tetrarhynchus paleaceus</i> RUD.	59. <i>Argulus coregoni</i> TROBELL.
30. <i>Tetrarhynchus spec.</i> Mc. INT.	Hirudinea:
31. <i>Tetrarhynchus spec.</i> ZSCHÖPKE.	60. <i>Piscicola geometra</i> LIN.
	61. <i>Cystobrancheus respirans</i> TROSCHE.

(7) The more mature the marine salmon is when entering fresh water to spawn, the more the individual number and the species of parasites are already reduced in the sea.

Table XIV

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Parasiten: Parasites	eigen: specific <sup>⊙</sup>	in ? □	in ? ×	Total	
1. <i>Derogues variatus</i> .		51	6	3	60
2. <i>Brachyphallus crenatus</i> .		17	4	—	21
3. <i>Hemisturus Lüheii</i> .		8	1	—	9
4. <i>Hemisturus appendiculatus</i> .		+?	3?	?	?
5. <i>Distomum reflexum</i> .		1	1	—	2
6. <i>Distomum Miescheri</i> .	+	—	1	—	1
7. <i>Distomum spec.</i>	+	—	1	—	1
8. <i>Sinistrophorus simplex</i> .		7	1	—	8
9. <i>Lecithaster gibbusus</i> .		22	4	—	26
10. <i>Azygia terticollis</i> .		—	2	10	12
11. <i>Crepidostomum farionis</i> .		—	3	5	8
12. <i>Abothrium crassum</i> .		—	8	20	28
13. <i>Bothriocephalus osmeri</i> .		—	2	—	2
14. <i>Bothriocephalus spec. I.</i>	+	—	1	—	1
15. <i>Bothriocephalus spec. II.</i>	+	—	1	—	1
16. <i>Bothriocephalus spec. III.</i>	+	—	1	—	1
17. <i>Bothriocephalenteron</i> .	+	—	1	—	1
18. <i>Bothriocephalus spec.</i>	+	—	1	—	1
19. <i>Taenia spec.</i>	+	—	1	—	1
20. <i>Tetrabothrium minimum</i> .	+	—	1	—	1
21. <i>Tetrabothrium spec.</i>	+	—	1	—	1
22. <i>Tetrabothrium spec.</i>	+	—	1	—	1
23. <i>Triacnophorus nodulosus</i> .		2	3	29	34
24. <i>Schistocephalus gasterostei</i> .		2	1	3	6
25. <i>Scolex pleurocæticus</i> .		more than th. 150	5	4	?
26. <i>Cocnomorphus grossus</i> .		24	3	—	27
27. <i>Tetrarhynchus quadrirostris</i>		11?	1	—	12?
28. <i>Tetrarhynchus crinæus</i> .		22	2	1	25
29. <i>Tetrarhynchus paluceus</i> .		42	1	—	43
30. <i>Tetrarhynchus spec.</i>	+	—	1	—	1
31. <i>Tetrarhynchus spec.</i>	+	—	1	—	1
32. <i>Ascaris clavata</i> .		26	2	—	28
33. <i>Ascaris ulanca</i> .		21	6	—	27
34. <i>Ascaris acuta</i> .		4	1	—	5
35. <i>Ascaris angulata</i> .		4	1	—	5
36. <i>Ascaris obtusocaudata</i> .		—	3	3	6
37. <i>Ascaris aculati</i> .		—	1	1	2
38. <i>Ascaris capsularia</i> .		92	9	3	104
39. <i>Ascaris communis</i> .		15	1	—	16
40. <i>Ascaris spec.</i>	+	—	1	—	1
41. <i>Ascaris spec.</i>	+	—	1	—	1
42. <i>Ascaris spec. I.</i>	+	—	1	—	1

Parasiten: P arasites	specific eigen?	in ? ○	in ? □	in ? ×	Total:
43. <i>Ascaris spec. II.</i>	+	—	1	—	1
44. <i>Ascaris spec.</i>	+	—	1	—	1
45. <i>Cucullanus elegans.</i>	.	1	5	18	24
46. <i>Neorhynchus rutili.</i>		—	3	29	32
47. <i>Neorhynchus agilis.</i>		8	2	—	10
48. <i>Acanthocephalus lucii.</i>		14	4	28	46
49. <i>Echinorhynchus gadi.</i>		51	5	6	70
50. <i>Echinorhynchus truttue.</i>		4	2	2	5
51. <i>Echinorhynchus salmonis.</i>		5	4	10	19
52. <i>Echinorhynchus heteracanthis.</i>	+	—	1	—	1
53. <i>Echinorhynchus spec.</i>	+	—	1	—	1
54. <i>Echinorhynchus spec.</i>		+	+	—	?
55. <i>Pamphorhynchus laevis.</i>		17	8	45	70
56. <i>Lepcophtheirus Strömi.</i>		—	+	+	?
57. <i>Lernaeopoda salmonca.</i>		+	+	—	?
58. <i>Lernaeopoda carpiónis.</i>		+	+	—	?
59. <i>Argulus coregoni.</i>		—	+	+	?
60. <i>Piscicola geometra.</i>		—	+	+	?
61. <i>Cystobranchnus respirans.</i>		—	+	+	?

Purely marine forms:	18
Marine-potamophilous forms	6
Potamophilous-marine forms	7
Purely potamophilous forms	10
Forms specific to salmon (marine?)	20
Total	61

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conclude that their starvation period does not depend on the change of medium, but is closely linked with their sexual development.

The fact that after spawning the descending salmon has occasionally freshwater parasites can be interpreted as a sign for the fish feeding in fresh water, although very little. This

again shows that feeding and starvation, respectively, do not depend on the change of medium.

The duration of the starvation period depends on the length of the sexual period; both coincide more or less with the stay of the fish in fresh water, as can be seen from the parasitic fauna, from its decrease in species and numbers of individuals, and from 132 its faunistic composition.

Temporal changes in the onset of the sexual period and the begin of the freshwater stay, and different lengths of these two periods are reflected in a change of the parasitic fauna.

(8) From a comparison of the faunistic composition of the parasitic fauna of Salmo salar in fresh water with that of the salmon in the sea it can be concluded that the salmon starves at least while ascending and spawning in fresh water.

The same result is obtained from physiological studies and findings.

(9) This applies above all to the Rhine, Elbe, Weser and Loire salmon. The parasitological finds in the Tweed and Tay salmon, on the other hand, admit a twofold interpretation: either the fish starve in the river (as in the Rhine, Elbe, Weser and Loire) or feed occasionally in fresh water.

(10) The statement that the parasitic fauna in the different media is a product of nutritional habits, also applies to Anguilla vulgaris, Alosa vulgaris, and several other migratory fish.

(11) Parasites are carried to other media by migratory fish, but in localities at great distances from the natural habitat of the parasites this results in acclimatization only in very rare cases and even then only temporarily.

At the boundary between the two media, in brackish water, a great exchange and permanent acclimatization of purely marine and purely potamophilous parasites can be observed. This renders the zoogeographical boundaries very indistinct.

(12) Parasitological-faunistic findings are of great value for nutrition biological and zoogeographical discussions.

Parasites are clear indicators for the life cycle of an animal. From them it is possible at any time to ascertain on what the animal feeds, where it lives, whether it suffers from scarcity of food or whether it lives in abundance.

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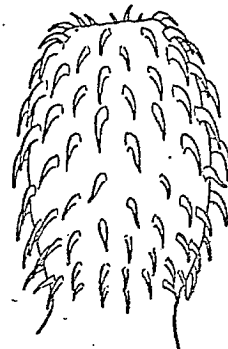
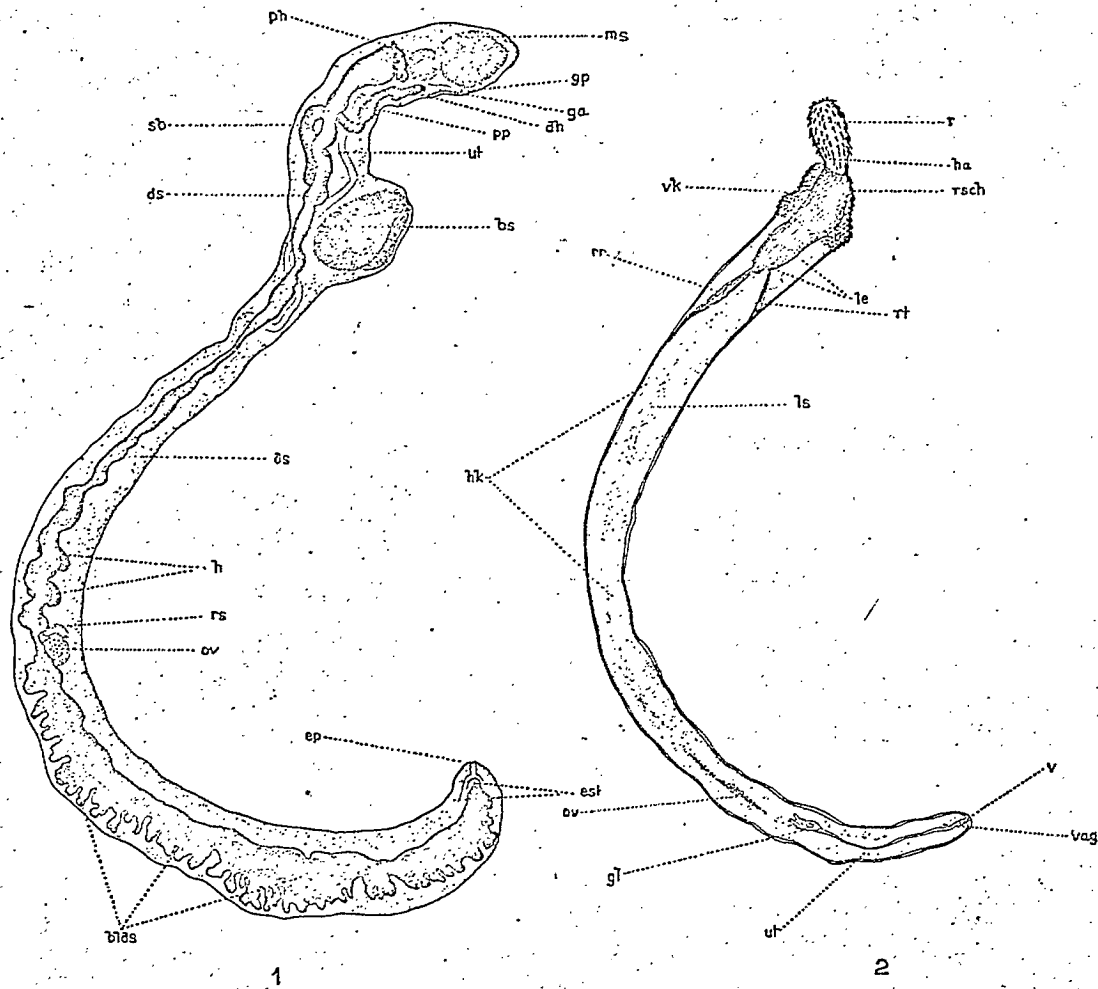
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Legend for Figures in Table

as = apical sucker	le = lemnisci
ak = protrusion canal	ms = oral sucker
b = bothria	oc = esophagus
blds = caeca of parts of intestine	ov = ovaries
bs = ventral sucker	ovd = oviduct
de = ductus ejaculatorius	ph = pharynx
dh = ductus hermaphroditus	pp = pars prostatica
ds = part of intestine	r = proboscis
eb = excretory vesicle	ro = rostellum
ep = excretory pore	rr = retractor receptaculi
est = excretory stems	rs = receptaculum seminis
fk = packed body (glandular cells)	rsch = sheath of proboscis
ga = genital atrium	rt = retinaculum
gl = bell-shaped uterus	sb = seminal vesicle
glt = pouches of bell-shaped uterus	sphv = sphincters of vagina
gp = genital pore	ut = uterus
glgr = base of bell-shaped uterus	v = vulva
h = testicle	vag = vagina
ha = neck	vk = anterior part of body
hk = posterior part of body	zgl = cells of bell-shaped uterus
ls = ligamentum suspensorium	

- Fig.1. Distomum Miescheri ZSCHOKKE, female
- Fig.2. Echinorhynchus heteracanthis nov.spec., female.
- Fig.3. Echinorhynchus heteracanthis nov.spec., female  
Female genitals. a - bell-shaped uterus, b - uterus,  
and vagina
- Fig.4. Echinorhynchus heteracanthis nov.spec., female.  
Proboscis
- Fig.5. Tetrabothrium nov.spec.
- Fig.6. Coenomorphus grossus (RUD.). a - according to HEITZ (1915); b - according to TOSH (1905); c - according to FRITSCH (1894). Natural size.

Taf. I.



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1880 -  
Helm's  
Organs

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